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AN ECOPHYSIOLOGICAL INVESTIGATION OF THE JACKPINE WOODLAND WITH REFERENCE TO REVEGETATION OF MINED SANDS

by

L.C. Bliss[1]
J.M. Mayo[2]

[1]Department of Botany, University of Washington
[2]Department of Botany, University of Alberta

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1.0 INTRODUCTION

To date, oil extraction from the oil sands utilizes the Clark Method, an alkaline hot water solution. This produces large amounts of alkaline sand which is stored in tailings ponds retained by a hydraulically built dike. One of the greatest environmental problems of this procedure is how to maintain the huge dikes of sand, keep them from eroding, and at the same time convert these seemingly barren mounds of sand and their hugh impoundments into useful production. The question is in effect, how to create a stable, self-perpetuating ecosystem? Much of the oil sands research has been directed towards this goal (e.g. Taki et al. 1977, Rowell 1977, Rowell 1978, Rowell 1979).

The early research by GCOS and most of the research sponsored by AOSERP within the Vegetation Subcommittee has centered on the use of agronomic grasses and on non-native shrub and tree species. Most of the species tested (Selner and Thompson 1977, Vaartnou 1976) are physiologically adapted to mesic habitats. As a consequence of using grasses not native to the dry and nutrient poor sands, it has been found that annual irrigation and fertilizer application are essential to maintain a dense plant cover. There has also been a high mortality of woody species, in part the result of stem girdling by small mammals.

This project was conceived as a multidisciplinary integrated study to determine the physiological limits of native and non-native species to dry, nutrient-poor environmental conditions on a steep-sided sand dike and on sand piles. Only when the limits of survival are known for native and non-native species, can there be a successful selection of species that will survive the unusually severe climate of a drought year that may occur every 25-50 yr. The chance of field trials falling within one of these severe drought years is small. Thus this project, via field and laboratory tests, was designed to determine the limits to growth of native and non-native graminoid and woody species under moisture and nutrient stress conditions.

The original objectives of this integrated study were: 1) to determine responses of pioneer and climax species to drought and nutrient stress conditions from field and growth chamber-greenhouse studies; and

2) via modelling the data on soil water and nutrient dynamics, micro and mesometeorology, soil microorganisms, tree water dynamics, lichen water relations, and the role of mycorrhizae of woody plants, be able to better predict the kinds of species and the density at which they can survive and maintain a plant community. The original intent was to include soil nutrient stress and to study plant responses on the GCOS dike. The nutrient and microbiological portions of this study were never funded and approval was not granted to conduct our proposed studies on the GSOC dike. Consequently, the project was changed considerably.

An extensive aerial survey resulted in the selection of a 30-35 yr Jack pine-lichen woodland at the Richardson Fire Tower. This vegetation was chosen because it is the dominant forest type on sands (level and steep slopes) in northeastern Alberta and northwestern Saskatchewan (Rowe 1959, Carroll and Bliss 1980). Open stand Jack pine is the natural end point of plant succession on porous sands and therefore a potential plant community to be maintained on the mined sands. The steep southwest-facing slope simulated a dike planted with Jack pine. Modelling was originally central to the project, but was reduced in emphasis to developing models of meteorological and physiological components with the reduction in funding. As a consequence the project became a more traditional one redesigned to determine how a Jack pine forest system adjusts to moisture stress in terms of the canopy trees, the lichen ground cover, and the role of mycorrhizae. A major assumption was (and is) that any species used to revegetate sand must withstand conditions of periodic drought. We believed that understanding the plant community(s) that stabilizes sand slopes in the Fort McMurray area would offer insights into the characteristics desirable in any species used to revegetate the mined sands. With the foregoing in mind, the final objectives of the study were:

1. To monitor the micrometeorological conditions in a Jack pine forest found to be stabilizing a sand slope at the Richardson Fire Tower.
2. To study water entry, movement and retention by a deep sand occupied by a native forest. This is important in predicting erodability and availability of water for plants.
3. To characterize the mycorrhizal flora of native species that stabilize deep sands in the Fort McMurray region and if possible understand their role in the plant community.

4. To describe the lichen flora of the pine forest and evaluate the role lichens play in the water regime of the community.
5. To study the water relations of Jack pine the dominant species found on sand slopes and evaluate its reaction to moisture stress.
6. To model radiation within the pine forest and develop energy and water balance models that could be used to predict tree behaviour. This later objective was greatly reduced by termination of the project.

Air and soil parameters were continuously measured within the forest and the response of Jack pine and lichens to environmental conditions was monitored for 25-48 hr periods. These intensive measurement periods were made during key seasonal development stages (spring snow melt, spring growth, mid and late summer, fall initial dormancy, and winter dormancy).

Additional research was conducted on burned forests and open sand dunes north of the Fire Tower. Jack pine forests of the region were also studied in relation to fire history.

The Jack pine-lichen woodland at the Richardson Fire Tower was chosen because it is the dominant vegetation type of sands (level or steep slopes) in northeastern Alberta, and thus the natural end point of plant succession on porour sands. The analysis of how this forest system solves its drought problems will be an aid in determining the desirability and feasibility of developing an open forest on the mined sands.

The information contained in this report represents a summary and synthesis of a much larger body of information provided in two earlier reports (Bliss 1977, 1979).

2.0 RESUME OF CURRENT KNOWLEDGE

2.1 SOILS

Information on moisture conditions in sands is limited because of their low economic importance relative to other soils. Because sands exhibit a high hydraulic conductivity at low moisture tensions and a very low hydraulic conductivity at high tensions, there is a fairly pronounced moisture level or "field capacity" to which they rapidly drain. Richards (1949) quotes 10.0 k Pa as the tension at field capacity for sandy soils while Russel (1961), Salter et al. (1967) and Webster and Becket (1971) suggest values closer to 5.0 k Pa. Some of the most recent work on moisture characteristics of sands has been carried out in Australia (Elrick 1963, Roberts 1966, Carbon 1975) where considerable variation is shown to occur, depending on sand size composition.

Considerable information about the properties of mined sand now exists (e.g. Cook, F.D.). The properties of mined sand, the effects of soil amendments such as peat, and vegetation responses have been studied by Takyi et al. (1977), Rowell (1977), Rowell (1978) and Rowell (1979). Comparison of their results with Richardson soils data is important in understanding revegetation and soil stabilizing criteria.

2.2 METEOROLOGY

There have been several major studies of the meteorology within forest canopies (Baumgartner 1965, Gay 1972, Landsberg and Thom 1971, Landsberg and Jarvis 1973, Mukammal 1971, Stewart and Thom 1973 and Thom et al. 1975). Because of the complex structure of the canopy, the actual micrometeorology of the forest is still not fully understood (Jarvis et al. 1976). In fact a recent workshop on forest meteorology (Hutchison 1979) stresses that "lack of knowledge and understanding of the mechanisms involved in turbulent exchanges of sensible heat, mass and momentum within forests and across forest-atmosphere interfaces is, without doubt, the most critical current problem of forest meteorology". Knowledge is not totally lacking, however. We have some understanding of unique features of the forest canopy such as the air flow within the trunk space area. From a number of studies involving flux-profile relationships it was found that the simple similarity relationships of other vegetated surfaces could not be applied to the forest canopy. The radiative properties of the forest are perhaps better understood than the turbulent processes. Several radiation components can be determined by means of mathematical models and computer techniques; and several studies have elucidated the variations of radiation within the canopy as well as the spectral properties of the leaves themselves. The major area which needs further research in forest radiation is the role of the structure and geometry of forests and validation of radiation theory and modelling with real data.

Nevertheless, in spite of the complexities of the forest canopy and the gaps in our present understanding a field research program was undertaken to support the main objectives of the revegetation-modelling project. The purpose of the project (see Introduction) was to provide management with information on our ability to predict the success or failure of different kinds of vegetation on raw sands. A first and practical revegetation problem was a tailings dike. This forced the selection of a site with slope, aspect and orientation similar to those of the G.C.O.S. dike. The choice of a sloped site eliminated all possibilities of having horizontal uniformity and consequently eliminated the use of flux-profile techniques and measurements which otherwise could have been used to understand some of the micrometeorological processes within the forest canopy.

2.3 MYCORRHIZAE

Mycorrhizae have repeatedly been shown to be necessary for normal growth of nearly all higher plants (Harley 1969) and the influence of mycorrhizae becomes increasingly important as environmental conditions become increasingly adverse (Schramm 1966). Schramm (1966) showed that ectomycorrhizae were necessary for successful survival of woody plants colonizing coal wastes that were characterized by hot, dry soil conditions. He found that few species of symbiotic fungi could tolerate these conditions of the site. Marx (1975) has shown that the use of *Pisolothus tinctorius* as a symbiont can significantly increase survival and growth of pines on these adverse sites. The work of Marx (1975) and others (Mikalo 1973) have shown that the symbiotic efficiency of fungi varies with environmental conditions and that inoculation of planting stock with fungi adapted to specific conditions can have a profound influence on growth and survival of plants.

Trappe (1977) suggests that mycorrhizae aid the host in water uptake and drought tolerance.

The mycorrhizal research at the Richardson Fire Tower site was aimed at defining the host-mycorrhizal relationships of *Pinus banksiana*, *Arctostaphylos uva-ursi* and *Hudsonia tomentosa* as they occur under natural conditions on sandy soils and applying this knowledge to revegetation problems on oil sands tailings.

2.4 LICHENS

In both mature and developmental plant communities on sand throughout North America, lichens frequently provide the major ground cover (e.g. Rowe and Scotter 1973). In the Athabasca Oil Sands region, extensive areas of sandy soils are covered with a Jack pine-lichen forest community. Any plant community allowed to develop naturally on the mined oil sands may therefore be assumed to have a considerable lichen component during at least one phase. Previous work on lichens in communities developed on sandy soils has shown that lichens may prevent the establishment of seedlings of trees and shrubs, and play an important role in water relations, acting as an effective barrier to water exchange between the underlying soil and the atmosphere (e.g. Rouse and Kershaw 1971, Jack 1935, Moul and Buell 1955). Heatmole (1966), and Rouse and Kershaw (1971) have examined water lichen relations in the field and Larson and Kershaw (1976) have carried out experiments in a wind tunnel. Lichens may therefore be a major factor influencing the establishment and maintenance of stable plant communities on the mined sands.

2.5 JACK PINE PHYSIOLOGY

A basic assumption in the study was that water is a major controlling factor in the long term stability of vegetation on sand. Accordingly physiologic research was concentrated on the major tree species Jack pine, *Pinus banksiana* Lamb. Mineral nutrition is recognized as an important limiting factor on sand, and the nutrition of Jack pine will be discussed.

Descriptive studies of the root system of Jack pine growing in sand have been conducted by Cheyney (1932) and Bannan (1980). In general the root system is shallow and wide. Several studies have been conducted on the nutrient composition of various Jack pine components (Morrison 1972, 1973, 1974) or the rate of transfer to the forest floor (Foster and Gessel 1972, Foster 1974). The addition of sulfur to the soils in the Fort McMurray area will alter nutrient cycling.

The cold hardiness of Jack pine has been studied by Yeatman and Holst (1972) and Glerum (1973). Jack pine is obviously hardy since it is native to the region, however provenances do exist and this must be considered in selecting for reforestation (e.g. Logan 1971). The water relations of hardy species is of interest. Most trees undergo winter dehydration with a considerable shift in osmotic potential (ψ_π) (McKenzie et al. 1974, Courtin and Mayo 1975). Wilkinson (1977) showed that *Ledum groenlandicum* undergoes considerable dehydration upon hardening and is easily cavitated whereas Jack pine does not cavitate. The degree of dehydration associated with winter hardiness is of importance in a system where there is limited available water in the soil and nearly half of the nonintercepted precipitation drains beyond the root system (see 5.1).

Many studies have been conducted on the growth responses of Jack pine and its close relative, lodgepole pine in response to environmental factors. These include nutrients (Cochran 1972, Calvert and Armson 1975, McClain and Armson 1975), air temperature (Cochran 1972), soil temperature (Heninger and White 1974), soil moisture (McClain and Arnson 1975) and rooting volume (Endean and Carlson 1975; Hocking and Mitchell 1975).

Legge et al. (1976) Dykstra (1974) and Lo gan (1971) have studied photosynthetic responses of lodgepole pine, but only Dykstra (1974) studied its response to drying and he did not study recovery. None of these studies dealt directly with Jack pine; thus a knowledge of its response to drought is of obvious interest.

Recently research on stomatal physiology has shown that the stomata of several species respond to vapor presure deficit independently of soil water potential (Sheriff 1977), and that some exhibit considerable control over transpiration in what is called a feedforward response (Farquhar 1978). Calder (1977) reported that sitka spruce is insensitive to soil moisture tensions up to 0.6 MPa and that the surface resistance to water loss, a term including leaf resistance (R_L), increased dramatically at VPDs ≥ 2.2 k Pa. Jarvis (1976) reported that the R_L of Douglas fir is relatively insensitive to xylem tension until 1.8 M Pa at which time R_L increases rapidly.

From the above it is evident that some plants are more conservative of soil moisture than others; i.e. they tend to have closed stomata prior to soil moisture stress induced closure. Pereira and Kozlowski (1977) have compared Jack pine and *Pinus resinosa* with respect to leaf water potential (ψ_L), leaf resistance (R_L), air temperature and VPD. Their work is of direct interest although limited in scope. Bennett and Rook (1978) report considerable difference in leaf resistance between two clones of *Pinus radiata* emphasizing clonal differences in drought hardiness and its importance in reforestation. Lopushinsky and Klock (1974) reported the effects of drying upon transpiration of lodgepole seedlings but only report transpiration as a percent of maximum. These studies, while useful, do not go into the water relations in sufficient detail nor do they refer to the lethal and sublethal limits of Jack pine, a major factor in successful long term stability on sand slopes.

2.6 MODELS

A major objective of VE6.1 was to develop mathematical models of energy and water exchange of a forested hillside, and to use these models to understand how trees survive under drought conditions. The interactions of solar and terrestrial radiation with vegetation are an important part of the energy exchange and a separate radiation model was a prerequisite for the larger energy and water balance models. *It needs to be stressed that the termination of the project did not allow for complete development of the models described below nor their application to the mined sands.*

2.6.1 Radiation Model

When the radiation intercepting elements (leaves, branches) are randomly distributed horizontally, a ray has a probability of penetrating to some depth without interception given by

$$P = e^{-F_c} \tag{1}$$

here F_C is the silhouette leaf and branch area per unit soil area in the layer above the level of interest. This result has been long known; the theory is reviewed by Norman (1975).

When Eqn. 1 is applied to the direct solar beam, P gives the fraction of horizontal area, at the level of interest, which is illuminated by the sun. When sky, or diffuse radiation is being considered, Eqn. 1 is used to compute radiation penetration separately from different directions, and the result is appropriately averaged to yield overall diffuse penetration.

The computation of F_c is often complex, depending on element area, number, shape and orientation, and direction of the ray.

Unfortunately, vegetation is rarely so ideally distributed that the Equation above can be used simply. Considerable literature is devoted to various methods of accounting for non-randomness of location, which may take the form of either clumping or uniform dispersal. Nilson (1971) pointed out that the Equation is the zero term in the Poisson distribution, and extended the scope of radiation models to include positive and negative binomial distributions. These distributions are empirical in that they contain an arbitrary parameter which must be adjusted to make the distribution fit the data.

For a sitka spruce plantation, Norman and Jarvis (1975) considered the clumping of needles into shoots and shoots into whorls using the Poisson distribution. Brown and Pandolfo (1969) analytically computed interception by identical cylindrical shapes that are regularly arranged on a flat surface.

Tanaka (1968) used a Monte-Carlo computer technique to compute interception by a tobacco plant community and Oikawa and Saeki (1972) used this technique to explore penetration in square-planted communities. This and other techniques for handling non-random distributions is reviewed by Monsi, Uchijima and Oikawa (1973).

Once the Equation, or some other approach, has been used to calculate solar beam and diffuse penetrations (and thus, interceptions), there remains the problem of the scattering of intercepted radiation. This very difficult problem has been approached in many ways, reviewed briefly by Norman (1975).

2.6.2 Energy and Water Balance Model

The purpose of the model is to predict the water status of the plants and soil, given a minimal input of environmental measurements. Since these predictions are desired over a wide range of conditions, it is necessary to use a mechanistic rather than an empirical model. Thus, the model must consist of mathematical equations pertaining to the mechanisms of atmospherical, biological, and physical interactions. The equations that were used were either obtained from literature, derived using our own theoretical developments, derived using data gathered by researchers in this project, or derived from data in the literature. The practical situation which was modelled (nonhomogeneous vegetation on a slope) is very different from the ideal (homogeneous vegetation on level terrain) on which most theoretical and experimental work has been concentrated. In fact, the only work done on a similar situation is that of Bergen (1969, 1971), and he considered only one special situation.

Most aspects which are unaffected by the slope can be modelled in ways similar to those reported in the literature. For example, the equations for the energy balance of needle clumps and the diffusion of water through the soil are commonly used (Murphy and Knoerr 1975, Goudriian and Waggoner 1972). However, the momentum and temperature of the air cannot be treated in any standard manner, since existing theory applies only to level surfaces. As previously mentioned, Bergen (1969, 1971) has made the only attempt to study temperature and wind speed on forested slopes. Also, modelling the water movement into and through plants, although unaffected by the slope, has not been solved satisfactorily (Gardner et al. 1975). However, in developing our model we have followed Jarvis' (1975) suggestion that the storage of water in sapwood is significant.

3.0 STUDY AREA

The Richardson Fire Tower site (Figure 1) (subdivisions 15 and 16, Sect. 30, Twp. 102, R6 W4 and subdivisions 1 and 2, Sect. 31, Twp. 102, R6 W4) was chosen because it is: 1) representative of pine-lichen woodland; 2) similar to a WSW sand dike slope, environmentally the most severe for plant growth; and 3) accessible via an airstrip. The hill slope (2.3:1 rise, 19° slope and 20° S of W aspect) has a porous sand which shows no evidence of surface erosion even with heavy summer rains.

This pine-lichen woodland, dominated by *Pinus banksiana* shows evidence of past fires, so characteristic of these forests on dry sites. A few scattered wolf trees are 60-65 years old, but the average age of trees is 30-35 years, and examination of a fire scarred older tree reveals that the slope was burned in 1930 or 1931.

Open stands of *Pinus banksiana* with a ground cover of lichens, mostly *Cladina mitis*, scattered dwarf shrubs of *Arctostaphylos uva-ursi* and a few forbs are characteristic of dry sandy soils in northeastern Alberta, northern Saskatchewan, and rocky sites of the Canadian Shield to the east and north (Rowe 1959). This region is termed the Athabasca South Section of the Boreal Forest Region. The only published account of these pine-lichen woodlands, but without quantitative data, are contained in the early paper by Raup (1935) on plant communities of Wood Buffalo National Park and Stringer (1976) on the vegetation of the oil sands region. The importance of fire in these northern forests is discussed by Rowe and Scotter (1973).

Two sets of plots were set up on the slope (Figure 2). All plots were 10 m on a side; the lower set includes 56 plots and the one above the trail contains 30 plots. Intensive meteorological sampling was confined to plot #47 (midslope); most of the physiologic studies of Jack pine and lichens were done in this vicinity.

A summary of tree data is contained in Table 1 for the lower set of plots and for the intensive plot. Trees are defined as stems 2 m high and/or stems 2 cm dbh at 1 m height. Five quadrats (1 m^{-1}) were sampled in each of four plots to determine ground cover. Ground cover in early October consisted of 1.4% herbs (mostly *Muhlenbergia cuspidata*); dwarf shrubs (8.7%), mostly *Arctostaphylos uva-ursi*; mosses 6.4% (mostly *Polytrichum poliferum*), lichens 47.0% (mostly *Cladina mitis*) and liter 36.7%. A list of vascular plant species is included in the Appendix (Table 13).

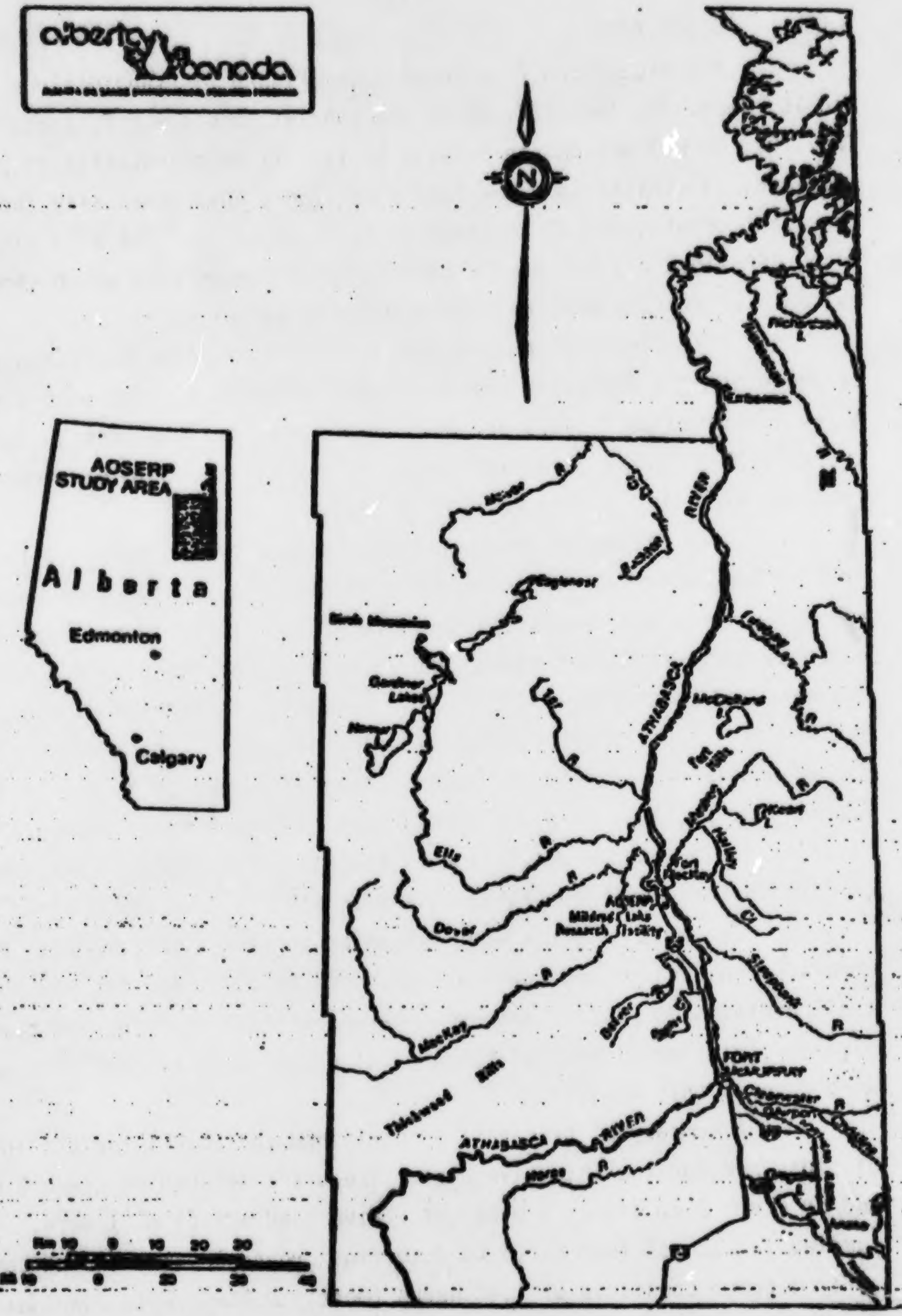
alberta canada
AOSERP STUDY AREA
Alberta
Edmonton
Calgary
N
Km 10 0 10 20 30
Birch Mountains
Gardiner Lakes
Namur L
ATHABASCA RIVER
Fort MacKay
AOSERP Mildred Lake Research Facility
Ells R
Dover R
MacKay R
Thickwood Hills
Horse R
Steepbank R
FORT McMURRAY
Clearwater R
Richardson L
Embarras
Fort Chipewyan

Figure 1. The AOSERP study area and Richardson Firetower site location map.

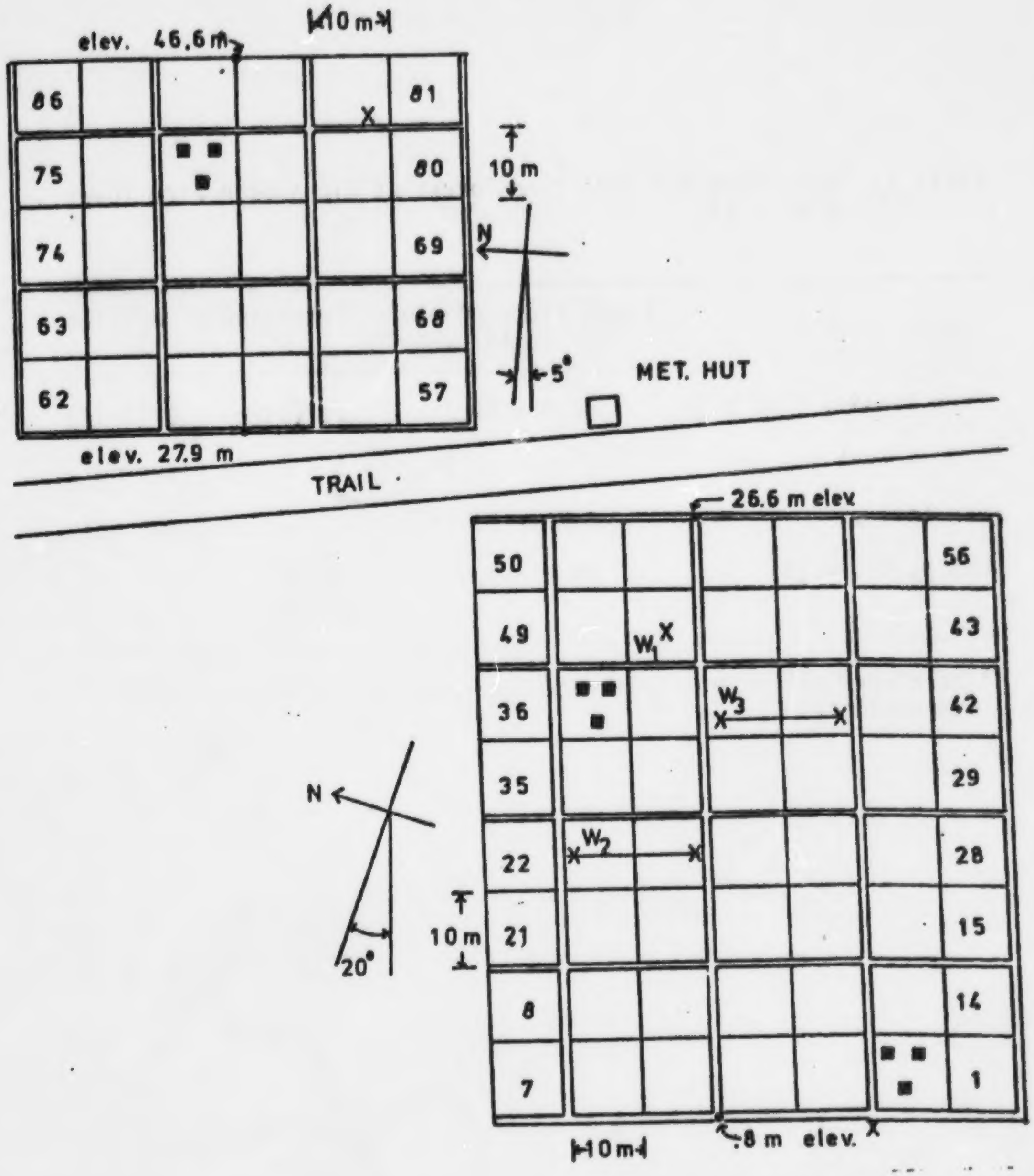
10 m
elev. 46.6 m
86
81
75
80
74
69
63
68
62
57
10 m
N
5°
MET. HUT
elev. 27.9 m
TRAIL
26.6 m elev.
50
56
49
W1
43
36
W3
42
35
29
N
22
W2
28
10 m
21
15
20°
8
14
7
1
10 m
8 m elev.

Figure 2. Study plots and instrument locations at the Richardson study site: X = meteorological towers; X—X = radiation transects; ■ = soil access tubes for neutron probe and thermocouples; W = profile sites.

Fig. 2

Table 1. Stand data for Jack pine forest at Richardson Fire Tower means ± SD.

Characteristic	Lower block of plots (n=56)	Intensive study plot #47
Tree Density (100 m)	62.9 ± 24.3	72 (live) + 9 (dead)
Tree Height (m)	(7.4 ± 1.2)*	5.4 ± 1.8 (live only)
DBH (cm)	6.75 ± 2.54*	4.8 ± 2.6 (live only)
Canopy Cover (%)	28.8 ± 9.0	35

*These were not determined by random sampling and are probably overestimates.

4.0 MATERIALS AND METHODS

4.1 SOILS

4.1.1 Laboratory Analyses

Particle size analysis was performed by the pipette method (Kilmer and Alexander 1949) with modifications made by Toogood and Peters (1953). Soil reaction was determined on a 1:2.5 soil:water mixture using a glass electrode. Total nitrogen was determined by the semi-micro Kjeldahl method (Bremner 1965). Calcium carbonate was obtained from inorganic carbon determinations using the method of Bundy and Bremner (1972), while organic carbon is the difference between total and inorganic carbon; total carbon having been obtained by combustion in a LECO induction furnace (Canadian Society of Soil Science 1975).

Cores taken in 2.6 cm diam. brass rings were used to obtain bulk density. With the possible exception of surface soil, bulk densities of sand are not easily varied, and it was found possible to obtain the same values as in the field by filling a ring closed at one end, with disturbed material while tapping the ring lightly on the table top. Because taking intact cores in the field without disturbance is very time-consuming, these laboratory-packed cores were used in certain determinations.

Saturated hydraulic conductivity was determined by the constant head method (Klute 1965). Rings (2.6 cm diameter, 6 cm long) were packed to a bulk density similar to that in the field and saturated with distilled water under vacuum. Because of the high permeability of the sands, it was necessary to minimize flow impedance by using 0.05 mm opening wire mesh screens at both ends of the ring in place of ordinary filter paper, while loss of fine material was minimized by reducing the quantity of water flow, by using micro-burettes at both the inlet and outlet ends of the core.

Unsaturated hydraulic conductivity was determined using an apparatus similar to that described by Elrick and Bowman (1964). Cellulose acetate filters of suitable pore size for the required pressure range were used at either end of similarly packed rings to those used for saturated conductivity. Pressures were controlled by drilling numberous small holes in the ring wall and enclosing the whole apparatus in a pressurized container.

Moisture retention curves in the range .001 MPa to .1 MPa have been obtained by the pressure plate method using small intact cores obtained with minimum disturbance in individual pressure cells. Liquid movement is slow in sands at low moisture content and therefore pressure plate results were found to be increasingly unreliable at higher tensions. Container thermocouple psychrometers (Korven and Taylor 1959) which depend on vapour movement, and function well only at higher tensions have however been used in the range .1 to 5.0 MPa. Several small 'chunks' from the same cores used in the pressure plate cells were partially dried in air and sealed in the psychrometer containers. These were then placed in a water bath. Microvoltmeter readings were made periodically until they stabilized (2 to 24 hr). The sand from each psychrometer container was then placed in weighing bottles for moisture determination by oven drying at 105°C.

4.1.2 Field Studies

Three field sites (Figure 2) were selected, one just below the top of the hill, one near the middle and one near the bottom of the hill, all close to meteorological recording sites and as closely as possible on the same contours while avoiding disturbed or non-typical areas. Monitoring was begun in November 1976. Each of the three sites was equipped with:

a) three neutron probe access tubes to a depth of 600 cm.

b) one set of copper-constantan thermocouples at 1, 2, 5, 10, 20, 50, 100, 150, 200, 300, 450 and 600 cm below the surface.

c) three sets of tensiometers at 20, 50, 100 and 200 cm, and one tensiometer at 300 cm.

Four more sets of thermocouples were added to the middle site at all depths between 1 and 100 cm, and one set of tensiometers was also added at 10, 20 and 30 cm below the surface. Two additional tensiometers were placed at 300 cm at this site, and three sets of psychrometers were installed at the lower site, between the lower and middle site, and at the bottom of the hill.

Thermocouples were read with a simple microvoltmeter using an ice-water mixture in a vacuum flask for a reference junction. The microvoltmeter was insulated from cold in winter. Tensiometers with mercury manometers, similar to those described by Webster (1966) were used. Normally they are useful in the range 0 to 0.08 MPa, however the low level of non-sand material at Richardson results in very slow liquid movement over most of the unsaturated range, with consequent large response times.

Very fine manometer tubing was used to minimize water movement into and out of the tensiometers, but their range of usefulness appeared to be still limited to 0 to .02 MPa. The large unfilled pore space in sand however favours good response from thermocouple psychrometers which depend on vapour movement. They are useful in the range .1 to 4.0 MPa, but only a few were installed. Tensions in the range .02 MPa to .1 MPa cannot be determined easily, and have to be inferred from moisture content using moisture retention curves.

Aluminium access tubes for the neutron probe were inserted in augered holes which were then backfilled around the pipe with the excavated sand. Counts of 1 minute duration were taken with a Nuclear Chicago P19 Neutron probe at depth intervals between 10 and 600 cm. Calibration was carried out by inserting similar, but shorter access tubes into augered holes, taking counts, and measuring the moisture content of the augered material gravimetrically. Since snow cover influences near-surface readings, the effects of snow depth and density on winter readings needed to be taken into account. For near-surface moisture determinations, the neutron probe has severe limitations because of its large sphere of influence, and it was therefore necessary to resort to gravimetric sampling.

Water wells measuring the water table were read by inserting and blowing down a measured plastic tube inserted into the well until bubbling was heard.

4.2 METEOROLOGY

The general approach to the measurement program reflected the dual purposes of the microclimate study. At one level a long term collection of some standard meteorological variables was undertaken in order to describe the climate and microclimate of the area and also to furnish the computer model with some essential atmospheric driving variables (Table 2). At a second more detailed level, frequent short-term measurements were undertaken during the so-called intensive runs (Table 2). The purpose of these intensive runs, which were normally of 24 to 48 hr duration, was to monitor the response of the trees and lichens to environmental conditions at key seasonal plant development stages (spring snow melt, spring growth, mid and later summer, fall initial dormancy and winter dormancy). These intensive runs also allowed us to better describe the plant-atmosphere

Table 2A. Continuous data logging system and sensors used to measure and produce atmospheric driving variables.

Sensor	Parameter measured
Eppley Precision pyranometer (280-2850 nm)	Global Incoming Radiation
Eppley Infra Red Radiometer (3500-50,000 nm)	Long Wave Incoming Radiation
Eppley Precision pyranometer (with filter 695-2850 nm)	Near Infra Red Radiation
Kipp and Zonen solarimeter (with shadow band)	Diffuse Sky Radiation
Kahlisco Radiation Balance Probe (300-6000 nm)	All Wave Incoming and All Wave Outgoing Radiation
Copper-Constantan Thermocouples	Air Temperature at 8 m Air Temperature at 0.05 m
Lambrecht Pernix Humidity Transmitter	Relative Humidity at 8 m Relative Humidity at 0.05 m
Climet Model 011-2b Anemometer	Wind Speed at 8 m
Stewart Electric Wind Vane	Wind Direction at 8 m
Weather Measure Tipping Bucket	Precipitation
Other variables	
C.S.I.R.O. Soil Heat Flux Plate	Soil Heat Flux
Copper-Constantan Thermocouples	Air Temperature near top of slope Air Temperature at bottom of slope Soil Temperature at 0.02, 0.08, .25 and 2.0 m
Lambda Quantum Sensor (400-700 nm)	Photosynthetically Active Radiation

Data logger: Campbell Scientific CR5 Digital Recorder
Data Recorder: D.C. Operated Facit 4070 Paper Tape Punch
Sampling Time: Integrated values over 30 min. period, printed every 30 min.

Table 2B. Data logging system and sensors used during intensive runs.

Sensor	Parameter measured
Eppley Precision pyranometer (280-2850 nm)	Global Incoming Radiation
Eppley Infra Red Radiometer (3500-50,000 nm)	Long Wave Incoming Radiation
Eppley Precision Pyranometer (with filter 695-2850 nm)	Near Infra Red Radiation
Kipp and Zonen solarimeter (with shadow band)	Diffuse Sky Radiation
Kahlisco Radiation Balance Probe (300-6000 nm)	All Wave Incoming and All Wave Outgoing Radiation
Copper-Constantan Thermocouples	Air Temperature 0.25, 0.5, 1.0, 2.0 3.0, 4.0, 5.0, 6.0 m Soil Temperature 0.01, 0.02, 0.04, 0.08, 0.125, 0.25, 2.0, 6.0 m

Data Logger: A.C. Operated Fluke 2240A
Data Recorder: A.C. Operated Facit 4070 Paper Tape Punch
Sampling Time: Every three minutes during intensive runs.

relationships and to assist in verifying and correcting the model.

Two special-purpose experiments were also conducted to help clarify the relationships between tree and canopy geometry and the unique atmospheric properties which are found within the forest canopy. The major experiment involved a series of radiation transects at several heights within the canopy and at two sites on the slope. Details of the radiation transect experiments are discussed in a separate section. The other special-purpose experiment involved measurements of precipitation interception by the forest canopy.

The first field season went from May, 1976 to early January, 1977. The second and final field season took place from March to August, 1977. Appendix 2 (1979 report) gives information on the time spans and dates of the field measurements of the continuous system, the intensive runs, and the profile and interception measurements. Figure 2 shows the location of the measuring sites on the hill as well as the general location of the hill.

In addition to the automatic acquisition of data during the intensive runs, vertical profiles of wind and water vapour were measured and recorded manually; every 14 min for the wind and every 15 min for the dew point. Sensitive RIMCO three-cup anemometers were installed at several heights and at three sites on the slope for wind profile measurements. There were some variations in anemometer-heights because it was not always possible to place the anemometers at exactly the same level at each site due to interference by branches. Specific heights are included with tables of results but generally the anemometers were at 0.5, 1.0, 1.5, 2.0, 3.0, 4.0, 5.0, 6.0 and 8.0 m. For water-vapour profiles a model 880 dew point hygrometer (Environmental Equipment Division) with four sensors was used. These sensors were installed at 0.5, 2.0, 4.0 and 6.0 m at each of the three profile measuring sites. Both anemometers and dew point hygrometers were on loan from the Meteorology Division, University of Alberta.

Precipitation measurements were made automatically using a Weather Measure tipping bucket raingauge attached to the Campbell data logger, and manually using a Taylor Clear View raingauge read at 0900 hr. Special investigations of precipitation interception by the canopy were also undertaken. Juice cans (48 oz) were used to measure interception at 11 sites on the hill. Whistance-Smith (1973) found that these were accurate raingauges. One can was placed in a clearing to measure the total amount of rainfall and two cans were placed at 0.5 m from the trunk of a tree. In addition, four trees were intensively sampled using radial lines of cans from near the trunk to the extremities of the branches. Cans were spaced at 0.25, 0.50, 0.75 and 1.0 m from the trunk along these lines. This allowed us to look at the variability of precipitation interception under the canopy.

Stemflow was measured by stapling and sealing 2.5 cm polyethelene tubing which had been previously cut in half, to the trunk, at diameter breast height (DBH). Whatever stemflow occurred would collect in a covered can attached to the tree. All cans were read as soon as possible after a precipitation event.

In order to understand radiation interception and reflection within the canopy, a radiation transect system was installed. This consisted of two supporting towers 20 m apart with four wire transect tracks stretched out between them. Three Lambda sensors (one pyranometer, one quantum sensor and one infra red sensor) were mounted on a small cart while three others were installed above the canopy on one of the supporting towers. As the cart travelled through the canopy during a transect, all sensors were monitored continuously. Many problems were encountered in forcing the cart to travel at a steady rate but these were solved. Several transects were measured in the latter part of the 1976 field season and several more in 1977.

4.3 MYCORRHIZAE

4.3.1 Species of Mycorrhizal Fungi Associated with Jack Pine

Sporocarps of fungi fruiting on the slope and in other Jack pine stands were collected in 1975 and 1976. Hypogeous fungi were usually found by observing where rodents had been digging and then raking the area. In addition, fungi were collected in stands of lodgepole pine in the Calgary area as these stands were readily accesible and the mycorrhizal associates of the two pine species are similar. A brief foray was also made in a lodgepole pine-bearberry stand situated on sand dunes on the Oregon coast. Although the climate is quite different in coastal Oregon than at the Richardson site, the soils and vegetation are similar.

In addition to the Richards Fire Tower slope, the mycorrhizae occurring in an area burned by wildfire in 1970 and regenerating to Jack pine was studied. This provided a comparison of the mycorrhizae in mature pine stands with pine on a recently disturbed area. The burn area lacked the *Cladina* lichen carpet characteristic of mature pine stands in the area. Bearberry and *Hudsonia* as well as some grasses were common plants on the burn.

4.3.2 Direct Isolation of Symbionts from Mycorrhizae

On the slope two 50 m transects were made, one through the lower plots and one through the upper plots. Soil cores, 5.3 cm diameter and 10 cm deep, were taken every meter for a total of 50 cores for each transect. In the burn a single 50 m transect was made along a slightly sloping south-facing ridge. The soils on both areas were very similar. Roots were much less frequent in the burn cores than on the slope; 25 pine root samples were taken from this transect. These were obtained by digging entire Jack pine seedlings, 0.5-1 m tall, shaking much of the sand off the roots and cutting off three lateral roots. The 15 cm sections of root were placed in plastic bags with some moist sand to prevent drying. The core samples were placed in plastic bags with moist paper towels and stored at 7-10°C for 5 to 6 days until they could be transported to the laboratory where they were stored at 2°C until they could be processed.

Each of the soil cores and root samples were washed free of soil and the roots stored in water at 2°C until they were plated. From each core sample three roots were randomly selected and five mycorrhizae from the end of each root were surface sterilized and plated. With the seedling roots, five mycorrhizae from each end of three roots were selected.

Nearly all of the mycorrhizae selected appeared to be on pine roots although some bearberry roots, which is indistinguishable from pine, may have been included. A few *Hudsonia* mycorrhizae were randomly included in the burn transect samples.

The mycorrhizae were surface sterilized by dipping in 95% ethanol, soaking in 30% H_2O_2 for 15 s and washing in an excess of sterile distilled water. The individual mycorrhizae were then placed on plates of MMN agar (Marx 1969), modified by the substitution of dextrose for sucrose and the addition of 100 ppm of Streptomycin, 50 ppm of Aureomycin and 5 ppm benomyl. In preliminary tests the addition of benomyl to the medium greatly enhanced the change of recovering possible symbionts. Its selective effects for basidiomycetes have been previously shown by Edgington et al. (1971) and Taylor (1971). The chance of benomyl eliminating mycorrhizal ascomycetes was probably nil as they rarely grow in culture (Trappe 1971) and *Cenococcum* was excluded from the otherwise random selection of mycorrhizal root tips. The plates were incubated at room temperature and examined after 1 and 2 months. All fungi that grew from the tips were considered possible mycorrhizal associates except phycomycetes. No hyphomycetes grew from the 3000 tips.

Representative isolates were subcultured and arranged in "species" groups. The range of cultural variation that was permited within each group varied and was based where possible (e.g. *Suillus* and *Rhizopogon*) on the variation observed on a range of isolates obtained from basidocarps. General colony morphology and the types, but not necessarily the amounts, of pigments appeared to the most reliable characters for separating different species. Macrochemical tests (Singer 1975) on the colonies including 10% KOH, Phenol-aniline, H_2SO_4 and NH_4OH were also useful with some groups. No positive results were found with phenol, $FeCl_3$, guaiaç or formalin. Chlorovanillin was useful in referring one set of cultures to *Lactarius* as specialized hyphal elements stained dark blue exactly like laciciferous and oleiferous hyphae in the Russulaceae (Singer 1975).

4.3.3 Identification and Abundance of Specific Mycorrhizal Types

In order to determine the importance of specific fungi as mycorrhizae formers, the ideal method would be a direct examination of the root tips. However, few mycorrhizae are distinctive enough to permit identification (fungus species + host; Zak 1973) or if they are distinctive, the fungal associate is usually unknown. Repeated attempts were made during the study to classify the mycorrhizae on the basis of morphology and colour. However, the majority of the mycorrhizae were a nondescript dull reddish brown to blackish and either monopodial or irregularily branched once or twice. This broadly defined type is thought to be formed by a large number of fungi based on our isolation studies. A similar type of mycorrhizae formed the surface cruse of *Elaphomyces muricatus* and *E. granulatus*.

4.3.4 Pure Culture Synthesis

Pure culture techniques were used to determine if specific fungi could form mycorrhizae with Jack pine. A variety of containers and substrates were tried in an attempt to find a method which would make the most efficient use of growth chamber space and to provide different growth conditions for the roots and shoots. The standard synthesis method in which the entire plant is enclosed in Erlenmeyer flasks places the tops in an unnaturally high humidity environment. The development of a technique with the tops exposed such as used by Trappe (1967) would provide a means to experimentally approach the effects of mycorrhizae on the water relations of seedlings.

4.3.4.1 Pure culture synthesis of Jack pine mycorrhizae. Preliminary techniques in large test tubes were described in the 1977 report. The mycorrhizal syntheses reported here followed the general procedure used by Zak (1976a). Syntheses were considered positive when a Hartig net or a Hartig net and an external mantle were present on hand cut sections and the symbiont could be recovered on MMN agar. Erlenmeyer flasks (1 litre) were partially filled with 420 ml vermiculite, 30 ml peat moss and 275 ml MN nutrient solution (Zak, 1976a) and autoclaved for 30 min. Jack pine seeds were soaked in cold running water for 24 h and surface sterilized by exposure to 30% H_2O_2 for 30 min. Seeds were placed on MMN agar plates and allowed to germinate. Contaminant free seeds with radicles 2-3 cm long were planted in the vermiculite-peat substrate. Each of five replicate flasks was then inoculated with 10 ml of a mycelial suspension from liquid cultures. One set of flasks was left uninoculated. Each culture was checked for viability and purity by plating on MMN agar plates. The flasks were placed in a growth chamber with an 18 h light - 6 h dark cycle. Temperature of the substrate did not exceed 22°C. After 6-12 mon the roots were examined for infection and contamination. Attempts were also made to synthesize mycorrhiza with *Hydnellum peckii* and *Elaphomyces granulatus*, two species which could not be cultured. Pieces of the basidiocarp of *Hydnelum* were surface sterilized in alcohol, flamed and placed beside roots of established pine seedlings. *Elaphomyces* ascocarps were surface sterilized, broken open and a spore suspension added to the synthesis flasks. A limited number of bearberry symbionts were tested in the same manner as Jack pine.

4.3.4.2 Pure culture synthesis of isolates from surface sterilized mycorrhizae. In the 1977 report 82 species groups were isolated from surface sterilized mycorrhizal tips. Only 11 of the 82 taxa could be related by cultural appearance to known mycorrhizal symbionts. It was thus unknown if a majority of these groups represented mycorrhizal fungi or were non-target, saprophytic fungi. In order to test the mycorrhizal forming ability, one representative of each of 18 groups was randomly chosen for synthesis trials in pure culture. Inoculum was prepared in vials containing MMN solution and broken glass fragments to fragment the mycelium (Zak, 1976a) so it could be injected aseptically onto the root system. Seedlings were grown in 150 x 25 mm test tubes in the vermiculite-peat-MN substrate as described in the previous report. The tubes were placed in a growth chamber and the roots examined for infection after 3 mon. Infection was determined by visual examination and confirmed by examining hand-cut root sections.

4.3.4.3 Growth of mycorrhizal fungi at different water potentials. In order to determine if different mycorrhizal fungi were adapted to low water potentials (ψ) they were grown on solid media adjusted to a series of osmotic levels with either NaCl or sucrose. The basal medium was MMN agar used by Mexal and Reid (1973) which they reported to have a water potential of -.16 M Pa. In the first test NaCl was used as the osmoticum and in the second sucrose was used to determine if there were specific ion effects of the NaCl. The desired molality values for NaCl were taken from a table in Kozlowski (1968). Osmotic coefficients and water activity values for sucrose were obtained from Robinson and Stokes (1955). Intermediate values not given in the tables were obtained from a linear regression between water activity and molality or water activity and water potential. Water potentials at 25°C were calculated by the formula by Griffin (1972); $\psi = -24.7\ VM\emptyset$, where V = ions/molecule, M = molality and $\emptyset$ = osmotic coefficient. Water activity (a_w) was converted to ψ by the formula by Griffin (1969) with

$$a_w = {}^{P}/_{PO}:\ \psi = \frac{RT \ln a_w}{10^6 M},\ \text{which simplifies to: } \psi = 1374.5\ (\ln a_w).$$

Plates were inoculated with either one or two agar discs taken from the margin of colonies growing in MMN medium. Three replicate plates were used with NaCl and four with sucrose. The inoculated plates were sealed with parafilm and placed in plastic bags to reduce moisture losses. Radial colony growth was measured at 10 day intervals.

4.4 LICHENS

The major lichen at the Richardson Fire tower is *Cladina mitis*. Accordingly field and laboratory studies of its water relations and its role in the water relations of the Jack pine forest were undertaken. Other studies included the geometric structure of the lichen canopy and the water relations of the duff layer.

4.4.1 Lichen Water Relations

Saturated solutions of various solutes were made to provide known relative humidities (Winston and Bates 1960). Lichen thalli or dead needles were suspended on wire hooks into the stoppers of the conical flasks containing the known saturated solutions. The flasks were then submerged in a water maintained at 20°C and allowed to equilibrate. After equilibration, wet and oven-dry weights were obtained and percentage water contents calculated. Water content was then plotted against water potential. Lichens were first saturated in distilled water for 24 h or air dried in the laboratory for 3 days.

In the field lichen samples were collected for gravimetric determination of thallus water content. Other samples placed in mesh pots (5 cm diameter) were weighed periodically to determine evaporation rates. The following parameters were recorded within the undisturbed lichen carpet: air temperature at 50 mm; lichen surface temperature at 7, 15, and 20 mm within the lichen carpet; soil temperature at the soil/lichen interface; and relative humidity at 50 mm. Temperatures were measured with copper/constanton thermocouples and relative humidity by a Thunder Scientific humidity sensor with signals recorded via a Fluke datalogger system.

Laboratory investigations involved the use of a wind tunnel. The lichen or duff samples were placed on a Mettler top loading balance, wind speed through the tunnel was controlled by adjusting the voltage to a fan and air flow was smoothed via tubular baffles (Figure 3). Wind speed was measured with a Hastings hot-wire anemometer. Radiation load was varied by placing floodlights at various heights above the window in the wind tunnel. Temperatures were measured with copper-constanton thermocouples and humidity with a Thunder Scientific humidity sensor.

At the start of a drying experiment, the plant material in the

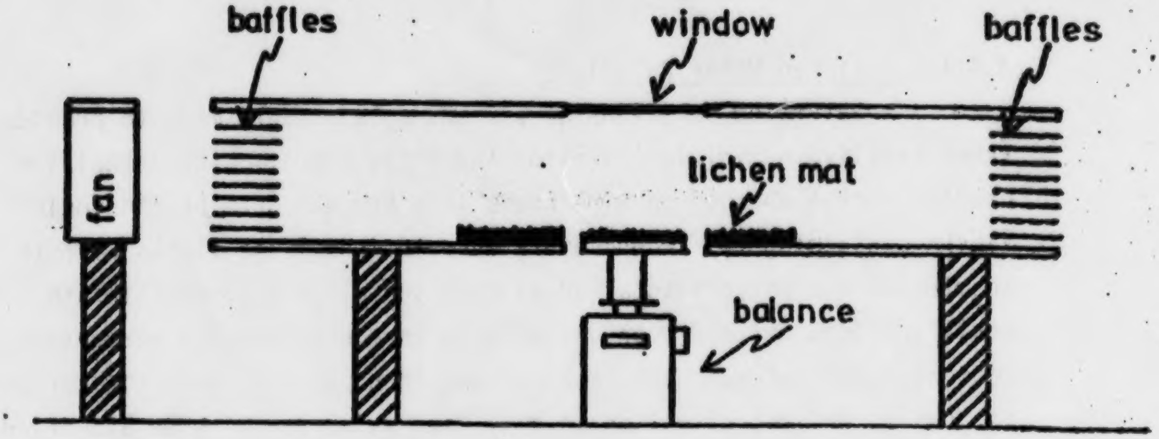
baffles
window
baffles
fan
lichen mat
balance

Figure 3a. Diagram of wind tunnel apparatus to determine lichen mat resistance to water loss.

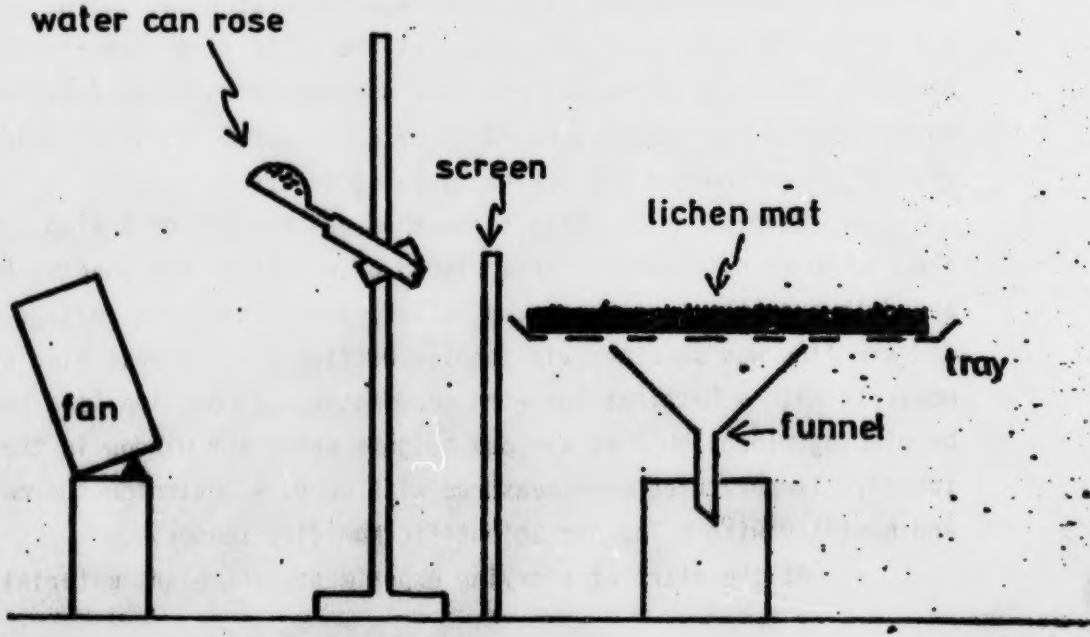
water can rose
screen
lichen mat
tray
fan
funnel

Figure 3b. Lichen rainfall interception apparatus.

wind tunnel was saturated with excess distilled water and allowed to drain. The central core of plant material was weighed at chosen intervals after slowing down the fan. Drying runs were carried out at several wind speeds to determine the influence of wind on boundary layer resistance. Experiments were also carried out in near darkness and with a radiation load of 3.2 w m^2 min^{-1} to assess the influence of radiation on drying rates.

From the following formula, it is possible to calculate total resistance of the plant material to water loss:

$$r_t + 1.138\ r_b = \frac{2\ (e_T - e_A)}{E(T_T^A + T_A^A)}$$

where: r_t = thallus resistance to water loss (min cm^{-1});
r_b = boundary layer resistance; = 2.17x10^{-4};
e_T = thallus vapor pressure; e_A = air vapor pressure;
E = evaporation rate (g cm^2 min^{-1});
T_T^A = thallus temperature (°K); and T_A^A = air temperature

Thallus vapor pressure (e_T) was calculated from:

$$e_T = e_o(T_T)\exp(\frac{T}{9.62T_T^A})$$

where: $e_o(T_T)$ = saturation vapor pressure at thallus temperature
ψ_T = thallus water potential; T_T^A = thallus temperature °K

4.4.2 Ground Layer Water Relations

Water uptake by the ground layer, lichens and/or duff was studied to determine how much rainfall it retains and its role in infiltration. Examination of the literature on rainfall simulators showed that such an apparatus has been designed primarily for field or large scale applications of rain and that no suitable apparatus had been designed for small-scale laboratory use. A watering can rose was used to produce raindrops of uniform size; the fall of these was randomized by use of an oscillator fan blowing at 2 m sec^{-1}. An aluminium tray with a fine mesh base was used to hold lichen carpet or needle duff with a plastic funnel 15 cm diameter placed centrally underneath. This funnel was supported on a sealed container (Fig. 3). The rate of rainfall was obtained by running the apparatus without any plant material in the mesh tray. Two rates were used, 2.2 mm h^{-1}, to simulate light and moderately heavy showers, the latter ca. the 25 yr maximum. Plant material was air dried and weighed before each run, weighed wet after each shower and the amount of infiltrate collected in the sealed container measured in a measuring cylinder. From the area of funnel and volume of infiltrate it is possible to calculate the amount of infiltrate in mm rainfall equivalent. From the duration and rate of showers it is possible to calculate total rainfall; thus the amount of rainfall intercepted and retained by the ground layer can be obtained.

Raindrop size was checked by the flour pan method (Steinhardt and Hillel 1966) and was found to be similar to natural raindrops, the majority being 2.5 mm diameter, with a range from 1.0-4.0 mm diameter. Terminal velocity was not determined, being considered relatively unimportant.

4.4.3 Other Studies

Other studies of lichens, reported in 1979, include: 4 studies of the lichen layer geometry and biomass distribution, penetration of PhAR penetration, emissivity, and albedo. These measurements along with the water relations studies were used to develop a model to predict behaviour of the lichen carpet under various environmental conditions. However, the model predictions did not satisfactorily agree with field data.

4.5 JACK PINE PHYSIOLOGY

4.5.1 Laboratory Studies

Leaf (needle) water potential (ψ_L) and xylem tension (-xylem pressure potential) along with water content were used to evaluate plant water status in both the laboratory and the field. Water potential is a measure of the free energy of water in a system, expressed in negative units of mega-Pascals (1 bar = 0.1 MPa). The components of water potential are:

$$\psi_L = \psi_\rho + \psi_\pi + \psi_\tau$$

where: ψ_L = leaf total water potential
ψ_ρ = turgor potential
ψ_τ = matric potential
ψ_π = osmotic potential

Leaf water potentials and component potentials were measured with thermocouple psychrometers after Mayo (1974). ψ_L was measured within 24 h of sampling then the psychrometer chamber was immersed in liquid nitrogen (-196°C) to rupture cell membranes and remeasured to determine combined osmotic and matric potential ($\psi_\pi + \psi_\tau$). Turgor ψ_ρ was estimated by difference in the equation. Xylem tentions (-xylem pressure potential) were measured with the Scholander pressure chamber (PMS Instrument Co., Corvallis, Oregon). Branches were collected and read within 30 min. Holding cut conifer branches in a high humidity container for periods up to 1 h does not introduce errors in measurement (Ritchie and Hinckley 1975). The Scholander pressure chamber, because of speed and ease of measurement, was the primary water relations instrument used in the field as well as the lab. The method has been thoroughly reviewed by Ritchie and Hinckley (1975). Water content of needles and stem segments were dried to a constant weight at 70°C.

The lethal and sublethal limits of moisture stress were studied by allowing potted (7.62 cm dia.) young trees (ca. 1½ yrs) to dry for predetermined periods, measuring xylem tension, ψ_L and $\psi_\pi + \psi_\tau$ then placing them in a humid greenhouse, watering and evaluating survival and damage at 3 and 15 weeks. The test plants had received the equivalent of two growing seasons prior to the experiment. During the drying experiment, the trees were kept in a growth chamber (E.G.C., Chagrin Falls, Ohio, U.S.A.) under the following conditions: Photoperiod, 14 h; PhAR (photosynthetically active radiation), 500 $\mu E\ m^{-2}\ s^{-1}$; 20°C; 75% RH (0.6 KPa VPD). Lamps were a mixture of cool white fluorescent 90% and incandescent (10%) based upon wattage. Drying times ranged from 4 to 15 days.

The effect of soil moisture stress (and recovery from near lethal levels) upon net CO_2 assimilation (NA) and dark respiration was studied by withholding water from young greenhouse grown trees over a period of days. These measurements were carried out using a computer controlled infra-red gas analyzer (IRGA) system designed by Dr. Whitfield. The Jack pine trees studied were potted young trees similar to those used in the lethal stress experiments described in the preceding paragraph. During the drying experiments the plants were kept in a growth chamber adjacent to the IRGA system under the following conditions: Photoperiod 16 h varied between 200 $\mu E\ m^{-2}\ s^{-1}$ and 600 $\mu E\ m^{-2}\ s^{-1}$ PhAR to simulate a daily maximum; 20°C; relative humidity >70% (<.7 k Pa). Water potential (ψ_L), NA, and water content were measured periodically as the trees dried the soil. When NA reached zero the intent was to rewater the plants and study them through another drying cycle. The same plants were studied through three drying cycles. The first cycle was not as severe as the second and NA was not followed to zero because of equipment malfunction. The second cycle was very severe in that the plants were ultimately stressed to a mean xylem tension of 3.5 MPa which we subsequently learned was near the lethal limit. One of the plants did not recover and had started to die when the experiment was completed. All of the NA measurements were carred out at 20°C, 540 $\mu E\ m^{-2}\ s^{-1}$ PhAR, and a mean VPD of 0.91 ± 0.08 KPa. Leaf temperatures were measured with 0.0076 cm (3 mil) copper constantan thermocouples and PhAR measured with a Lambda (Lambda, Lincoln, Neb., U.S.A.) quantum sensor.

4.5.2 Field Studies

Water potential and its components, xylem tension, and water contents were measured as described under Laboratory Studies (4.5.1).

Transpiration rates were measured by a technique of measuring the increase in absolute humidity of air passing over a transpiring branch (Slavik 1974). Humidity was measured with a dew point hygrometer (EG & G 880). Leaf area was determined using the glass bead technique of Thompson and Layton (1971). Transpiration may be used to calculate the diffusive resistance to water loss according to Slavik (1974):

$$R_L = [(C_{sat} - C_a)/q] - R_a$$

where R_L = leaf resistance in $S\ cm^{-1}$; C_{sat} = saturation absolute humidity at leaf temperature; C_a = absolute humidity at air temperature; q = transpiration rate; and R_a = leaf boundary layer resistance estimated according to Nobel (1974);

$$R_a = \alpha^a/D_j$$

where D_j = diffusivity of water vapor; α^a = boundary layer thickness estimated from:

$$\alpha^a = 0.4\ (l_{leaf}/V_{wind})^{1/2}$$

where l = the leaf dimension in the down wind direction; and V = wind velocity.

Leaf and air temperatures were measured with 0.0076 cm diameter copper-constantan thermocouples and a Fluke digital thermometer (model 2100A).

Leaf resistance was also studied with a diffusive resistance porometer based upon that of Gresham et al. (1975). This method does not measure transpiration rate, but is considerably faster and provides information by needle age class. It was used almost exclusively in 1977.

4.6 MODELS

4.6.1 Radiation Model

The natures of both the site and vegetation type introduce complexities into the model. The site is a steep hillside, while most detailed radiation models have been applied to flat sites; the leaves are doubly clumped into tufts on branch ends and into discrete trees, often well separated from their neighbours. Thus the situation is greatly different from the ideal simple case of a horizontally random distribution of intercepting surfaces. The model is based on an innovative technique in which a Monte-Carlo simulation is used to calculate the interceptions of light rays with idealized tree outlines, following which the usual theory of interception by randomly located elements is applied along the ray paths within trees.

For the sake of clarity, the model is not described in great detail. The reader is referred to the 1979 AOSERP report for a complete treatment. SI units are used throughout, except where noted otherwise.

The situation was idealized as follows:
(1) the hillside is a flat plane of slopes, from horizontal and azimuth w_s. Figure 4 illustrates this geometry; (2) the trees are randomly located with their trunks vertical (at angle α_s to a normal to the slope; (3) tree heights are random; (4) each tree is cylindrical and flat topped or cone capped; and (5) all vegetational elements (needled branches, bare live branches and cones) are randomly located within the shape being horizontally uniform and vertically distributed according to empirical measurements of an actual tree.

The model then determined:

(1) The penetration of diffuse or sky radiation into the canopy of a numerically random canopy:

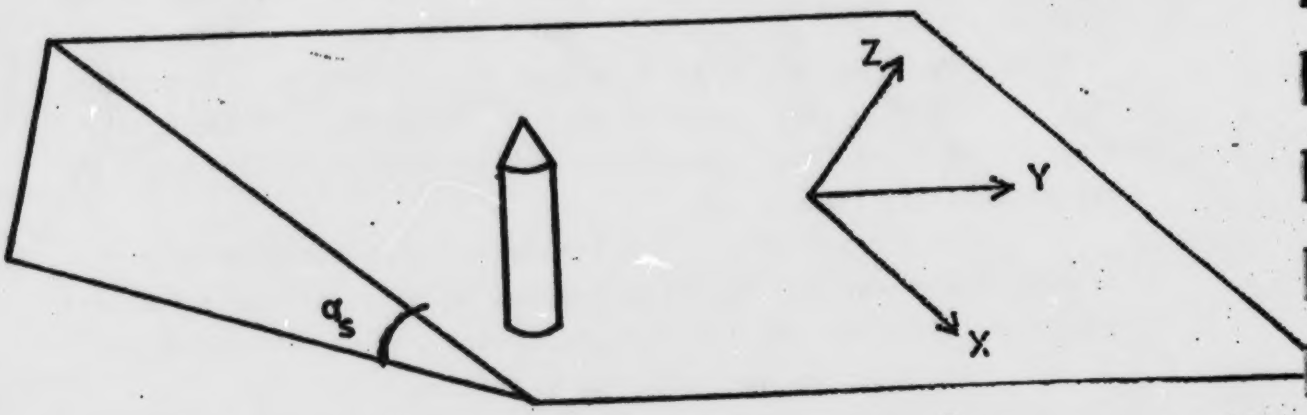

Figure 4. The idealized hillside used in the model with an idealized tree and the co-ordinate system used.

$$\overline{P}_i = \frac{\int_0^{\pi/2} d\eta \int_0^{\pi} d\phi \quad \Gamma(\eta,\phi)\, \hat{P}_i(\eta,\phi) \sin\eta \cos\eta}{\int_0^{\pi/2} d\eta \int_0^{\pi} d\phi \quad \Gamma(\eta,\phi) \sin\eta \cos\eta}$$

where: η = zenith; ϕ = azimuth; $\Gamma(\eta,\phi)$ = relative sky brightness in η,ϕ direction (Γ); and $\overline{P}_i$ = the probability of noninterception of radiation (the equations used to obtain $\overline{P}_i$ are in Appendix).

(2) The calculation of the scattering of intercepted radiation was handled after Norman and Jarvis (1975). These calculations resulted in a series of tables of scattered radiation above each height level including the ground surface, downward and upward, originating from direct solar beam and diffuse sources for visible and near infrared wavelengths. Tables of radiation absorbed were also produced.

(3) Total downward radiation flux:

The first step in this calculation is partition of incoming radiation into four components by two ways of division: direct vs. diffuse, visible vs. near infrared. The measured quantities were total all-wave, diffuse all-wave and total infra-red. Then the diffuse all-wave (S_d) may be divided between visible and infrared components.

$$S_d^v = 0.7\ S_d$$

$$S_d^r = 0.3\ S_d$$

which follows Ross (1975). The beam components then follow directly from the above and the measured total all-wave (S_t) and total infrared (S_t^r)

$$S_b^r = S_t^r - S_d^r$$

$$S_b^v = S_t - S_d - S_b^r$$

Then, given the sun position, η, ϕ, we can write down the desired downward fluxes at the bottom of canopy level i as fractions of their values at the canopy top (V_i for visible, R_i for infrared):

$$V_i = \{\varepsilon\ [S_b^v\ (E_i^{bv}\ (\eta,\phi) + \hat{P}_i\ (\eta,\phi) = S_d^v\ E_i^{dv}\ (\eta,\phi)]$$

$$+ (1 - \varepsilon)\ [S_b^v\ E_i^{'bv}\ (\eta,\phi) + S_d^v\ E_i^{'dv}\ (\eta,\phi)]\}/(S_b^v + S_d^v)$$

and

$$R_i = \{\varepsilon\ [S_b^r\ (E_i^{br}\ (\eta,\phi) + \hat{P}_i\ (\eta,\phi) + S_d^r\ E_i^{dr}\ (\eta,\phi)$$

$$+ (1 - \varepsilon)\ [S_b^r\ E_i^{'br}\ (\eta,\phi) + S_d^r\ E_i^{'dr}\ (\eta,\phi)]\}/(S_b^r + S_d^r)$$

where ε is the weighted proportion of the horizontal sensor's hemisphere which sees downward scattered radiation. This enters into the calculation because of the angle α_s between the hillside normal and a normal to the sensor. The value of ε for $\alpha_s = 22°$ is 0.9633.

The method used to actually measure radiation was similar to that of Norman and Jarvis (1974). We established vertical towers ca. 20 m apart, 9 m high, aligned across the slope. At chosen heights, wire pairs, 15 cm apart in a hortizontal plane, were stretched taut between the towers. A teflon-skidded sled, 18 cm x 18 cm, bearing horizontally mounted sensors, was towed at a uniform speed along the wires from tower to tower. A data acquisition system periodically recorded the signal from the mounted sensors and from similar sensors mounted horizontally atop one of the towers. The sled speed and recording interval were such that readings were made approximately every 2.0 cm along the transects.

Two different sensors were used, both manufactured by the Lambda Instruments Corp. One sensor, model LI-190S, responds nearly equally to photon numbers in the wavelength band 400-700 nm., with nearly zero response outside this band. The other, model LI-220S responds to band about 70 nm wide around 780 nm. The sensors were terminated by appropriate resistors supplied by the manufacturer.

In our processing of the data logger output, we computed for each set of readings the ratio of sled sensor to tower sensor values, and averaged these ratios along the transects. These average values are the basic data for comparison with model output. Two transect stations (Figure 2) were used with four levels run at one and three at the other.

4.6.2 Energy and Water Balance Model

Since the conditions in the atmosphere, plants, and soil vary with height, we must consider interactions at different levels. The microclimatic factors of radiation, temperature, humidity and wind are determined at different levels in the canopy. Then it is possible to calculate the temperature of sunlit and shaded leaves at different heights on the trees. This leads to transpiration at different heights, and integration over height yields total transpiration. This results in a change in average needle water potential and a flow from sapwood to needles. This in turn results in a change in the sapwood water potential and a proportionate flow from the soil into the sapwood. Now the roots are distributed in a certain vertical pattern in the soil so extraction of water from the soil is not uniform over depth. Therefore, we keep track of the soil water potential at different depths. Thus, the equations for radiation, wind speed, air and needle temperature, and soil water potential are solved at several levels, whereas the equations for the water potential of the sapwood and needles are solved once for an average value for the tree. A simplified flow chart of the model is given in Figure 5. The equations are given in Appendix 1/1977 Report.

The pattern of distribution and the amount of needle area in the canopy is based on preliminary measurements of the physiologists. View factors of one level of the canopy for another are calculated with a negative exponential function of needle area and a suitable effective area fraction. This results from treating the needle area as randomly distributed which allows treating penetration through the canopy as a Poisson process. However, since the needle area is not random but is clumped to some degree, actual penetration will be greater than expected. Thus, we insert a clumping factor into the negative exponential function to allow for increased penetration. View factors are calculated for diffuse radiation and are used for diffuse shortwave penetration from the sky into the canopy, for shortwave scatter within the canopy, and for longwave radiation transfer.

Shortwave radiation is divided further into direct and diffuse PAR and direct and diffuse NIR. From three measurements at the top of the hill, the four types of shortwave radiation are calculated using formulae derived from data of Sceicz (1974). The actual amount of diffuse

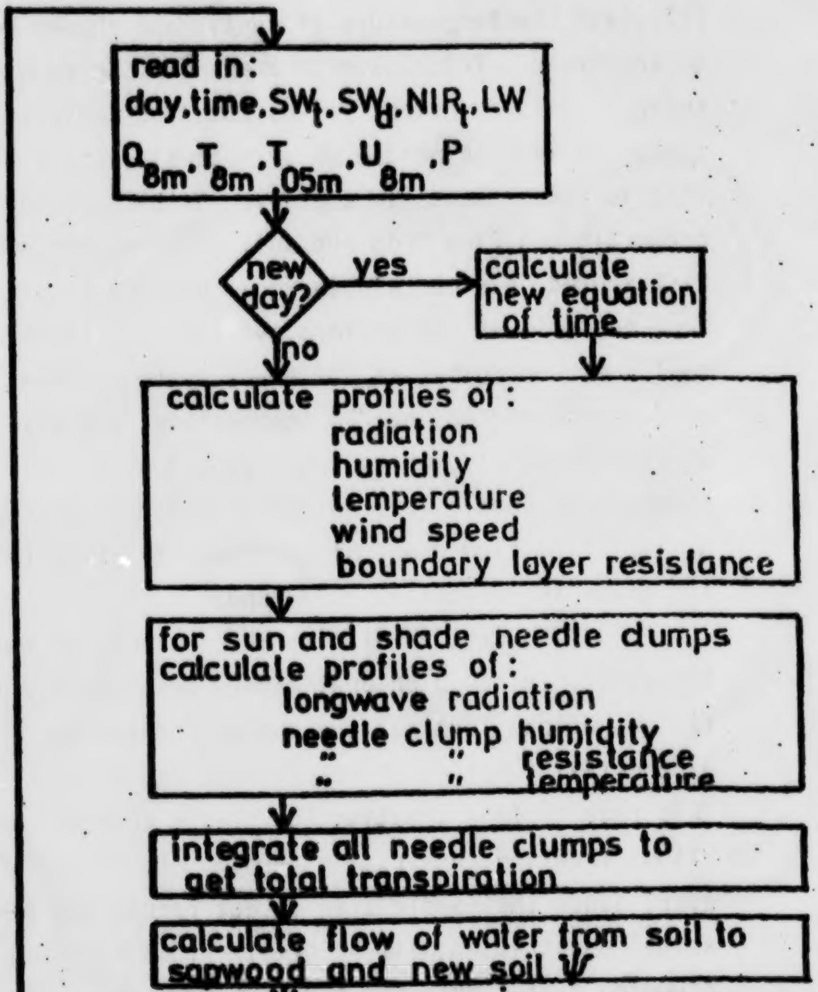
read in:
day, time, SW_t, SW_d, NIR_t, LW
Q_8m, T_8m, T_.05m, U_8m, P
new day?
yes
no
calculate new equation of time
calculate profiles of:
radiation
humidity
temperature
wind speed
boundary layer resistance
for sun and shade needle clumps calculate profiles of:
longwave radiation
needle clump humidity
" " resistance
" " temperature
integrate all needle clumps to get total transpiration
calculate flow of water from soil to sapwood and new soil Ψ
calculate water flux sapwood to needle clump, and new sapwood and needle clump Ψ

Figure 5. A simplified flow diagram of the water balance model.

radiation intercepted by the slope comes from the sky and from reflection off the forest on the plain below. The angle of incidence and the azimuth of direct radiation intercepted by the slope is a complex function of the latitude and longitude of the site, the slope and aspect of the hillside and the year, day, and time. Equations are derived using data from the American Ephemeris for 1974 and using equations for Gloyne (1965).

The amount of direct radiation penetrating to any level in the canopy is the intensity of radiation from the sun times the view factor for direct radiation at the angle of incidence. The amount of diffuse radiation impinging on the hillside times the view factor, plus the sum of the reflected direct radiation from other levels in the canopy.

Finally, we can calculate the shortwave radiation absorbed per m^2 needle surface area for needle clumps in direct sunlight and needle clumps in the shade. It is important to note that all of the view factors and penetration probabilities can be calculated independently of the rest of the model and the results stored in an array which can be quickly referenced by the model.

The air temperature at any level in the canopy is approximated by the average of the temperature at canopy height and the value resulting from a line drawn from the temperature at canopy height to the temperature at 5 cm above the lichen carpet. We have resorted to this empirical approximation because there is no theory for heat transfer in a non-homogeneous plant canopy on a slope. Indeed, the equations using eddy diffusivity which have been applied to homogeneous canopies on level ground do not produce entirely satisfactory temperature profiles (Mehlenbacher and Whitfield 1977). However, the crude approximations used here do provide us with fairly good temperature profiles as seen in Figure 6.

The air specific humidity profiles are surprisingly constant and so the specific humidity at any level can be approximated by the specific humidity at canopy height (Figure 6).

Wind speed is exponentially attenuated into the canopy.

The temperatures of the sunlit and shaded leaves at each level are found as solutions of energy balance equations of the form

$$ASW + ALW = p_a C_p \frac{(T_n - T)}{r_b} + p_a Lt \frac{(Q_n - Q)}{r_b + r_n}$$

ASW is absorbed shortwave radiation, T is °K, and Q heat. So now we shall discuss in turn the air density (p_a), heat capacity (Cp) latent heat of vaporization (Lt), needle clump boundary layer resistance (r_b), needle clump transpiration resistance (r_n), andnet absorbed longwave radiation (ALW).

Air density is a function of air temperature derived from measurements in List (1966), and heat capacity is considered constant. The latent heat of vaporization for water in a needle clump is a function of needle clump temperature adapted from Murphy and Knoerr (1972). Needle clump boundary layer resistance has been determined as a function of wind speed for ponderosa pine needle clumps by Gates et al. (1965).

Transpiration resistance has been studied quite intensively by the physiologists. It is a function of intensity of PhAR, vapour pressure deficit, and water potential of the needles. Therefore, resistance is calculated separately for sunlit and shaded needle clumps. Figure 5 shows that transpiration resistance increases with decreasing PhAR, with increasing VPD, and with increasing ψ_{leaf}.

The net longwave radiation at any level is a function of the longwave radiation lost by emission proportional to the needle clump temperature at that level. Therefore, it is also calculated separately for sunlit and shaded leaves. It is also a function of the longwave radiation emitted by the sky, the needle clumps at other levels, and the lichen mat, and the view factor of these sources for the level being considered.

The needle clump temperatures are obtained by an accelerated iterative solution of the energy balance equations. Then the specific humidity is obtained using an equation from Murray (1967).

The plant water environment has been partitioned into two compartments - sapwood and needle clump. The flow of water from the soil into the sapwood is the sum of the flows from the soil layers, which are functions of the sapwood water potential, the water potential and root area of the soil layers, and the root resistance. The flow of water from the sapwood into the needles is a function of the sapwood-needle water potential gradient and the sapwood resistance. Total loss of water from the needles to the air is the sum of transpiration from sunlit needles and shaded needles. Each of these is the sum over all layers in the canopy of a function of

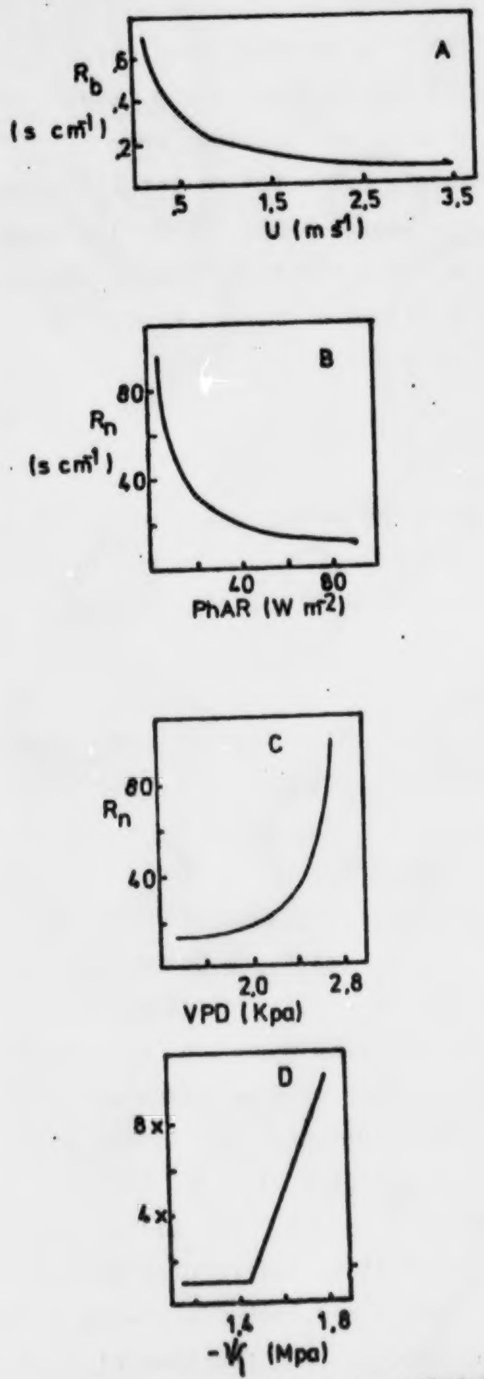

Figure 6. Model parameters estimated from physiologic studies: A) leaf boundary layer resistance (R_b) vs windspeed (U); B) needle clump leaf resistance (R_n) vs photosynthetically active radiation (PhAR); C) needle clump resistance (R_n) vs vapor pressure deficit (VPD); D) needle clump resistance (multiples of R_n minimum) vs water potential (ψ_l).

air and water density, needle clump-air specific humidity gradient, boundary layer and stomatal resistance, and needle area in the layer.

The dry weight of sapwood per m^2 area was obtained from estimates of sapwood radius (from R. Swanson), estimates of total tree volume, and the approximate density of Jack pine sapwood. The soil water potential is considered in the next section, and the distribution of root area is a reasonable estimate. Reasonable values of r_r and r_t can be obtained since assigning a steady state, we have

$$E = \Delta t \frac{(\psi_t - \psi_n)}{r_t} = \Delta t \sum_i \frac{(\psi_{s,i} - \psi_t)}{r_r} A_{r,i}$$

Using model simulations to obtain value of E and measurements of our plant physiologist and soil physicist we find that r_t and r_r are on the order of 10^{13} Psm^{-3} kg. The boundary layer and stomatal resistance have been discussed in the energy balance section.

As a result of the flow of water along potential gradients, the water content of each compartment changes during each time interval. The change in water content of the sapwood is the difference between the flow in from the soil and the flow out to the needle clumps. The change in water content of the needle clumps is the difference between the flow in from the sapwood and the flow out to the atmosphere. These changes in water content are added to the old water contents and updated water potentials are determined using a linear empirical formula based on measurements of the physiologists.

At the start of the simulation we are provided with the profile of soil water potentials, and then at half hr intervals we calculate the change in ψ_s, i resulting from uptake by the plants and from diffusion. Daily precipitation which penetrates through the Jack pine and lichen canopy is added into the soil water budget at midnight. Not all of the precipitation enters the soil system. Much of it is intercepted by and subsequently evaporated directly from the needle and lichen surfaces. The amount of precipitation intercepted by the needles is a function of interception of precipitation impinging directly on the needles and overflow from needles above. An empirical function of interception by the trees in terms of rainfall intensity has been derived using data of the meteorologists. The lichenologist has provided a good average for interception by the lichen mat and needle duff. The water reaching the soil is distributed over the soil layers, assuming the top layer is filled to field capacity, then the next layer down, and so on. Water retention curves for 0 - .075 m, 0.75 m - .15 m, .15 m - .35 m, and .35 m + are stored in a table, and at each time interval the current $\theta_{s,i}$ is found by interpolation from the table using the current $\psi_{s,i}$. Now we are ready to consider the change in volumetric soil water content due to root extraction and diffusion. The change due to root extraction is a function of the sapwood-soil water potential difference, the root surface area, and the root resistance to water uptake. The change due to diffusion is a function of changing water potential with depth and hydraulic conductivity. The diffusion equation is a partial differential equation solved by finite differencing, while the hydraulic conductivity is a function of the water content. Finally, the new water potential is obtained by looking up the soil water potential in the tables corresponding to the water content $\theta_{s,i} + \Delta\theta_{s,i}$.

5.0 RESULTS

5.1 SOILS

The soils at the Richardson Site are Eutric Brunisols. The litter and H layers are both thin, their combined thickness ranging from 1 to 3 cm. Beneath the H layer is an Ae horizon, which although almost absent in places, is more than 15 cm thick on the lower slopes. This overlies a Bm horizon which is approximately 20 cm thick, this in turn merges into the very pale brown loose sand of the C horizon.

The sand is mainly medium to fine but variations occur, lenses of finer and more coarse material in many places being interwoven. Occasionally a lens high in silt is encountered, but generally non-sand material is very low. There are a few boulders 5 cm to 50 cm across, but these seem too few to affect water movement.

5.1.1 Laboratory Analysis

The particle size analysis (Table 3) indicates a fairly even distribution between the medium and fine fractions and the near absence of anything but sand. There is also a conspicuous absence of calcium carbonate and pH is low except in the deep samples. Bulk densities range from 1.35 to 1.95 in the Ae horizon to 1.5-1.6 in the C horizon.

Saturated hydraulic conductivities (Table 4) are extremely high, particularly at the surface. Hydraulic conductivity - moisture content curves using the Millington and Quirk equation (1961) matched to laboratory values (Green and Corey, 1971) are given in Figure 7. Laboratory determined conductivities show a reasonable approximation to theoretical values.

Moisture retention curves for the various soil horizons at the middle site are given in Figure 8. The top and bottom of the hill sites were no different, thus Figure 8 is representative of the whole hillside. If .005 MPa is taken as the tension at which rapid drainage of the C horizon ceases, moisture content (by volume) would be 10%. Field moisture values were 6% when determined soon after periods of rain. Thus 'field capacity' is taken as .006 MPa and agrees with other values reported for sands (Salter et al. 1967, Webster and Becket 1971). Since ca. 0.2% moisture remains in the sand at high tensions, 5.8% moisture is available for plants. This corresponds to 58 mm of water per meter of sand which is quite low. The 0-5 cm soil is much greater being 95 mm m^{-1} while the B_m horizon is intermediate.

Table 3. Particle size distribution and chemical analyses of sand from the Richardson sites.

			% Sand Fractions											
Site	Horizon and depth (cm)		VCS (>1 mm)	CS 1–0.5 (mm)	MS 0.5–0.25 (mm)	FS 0.25–0.105 (mm)	VFS 0.105–0.053 (mm)	% silt 0.053–0.002 (mm)	% clay <0.0002 (mm)	pH	Organic carbon (%)	Nitrogen (%)	$^C/_N$	$CaCO_3$ eq %
1	C	50	0.1	4.2	56.7	36.9	1.8	0.1	0.3	6.3	ND	ND	ND	0.0
	C	600	0.2	4.5	40.3	39.7	9.2	5.3	0.9	8.2	ND	ND	ND	0.0
2	Ae[a]	0–2	0.3	5.7	38.0	45.9	7.3	2.3	0.5	4.8	0.74	0.022	34.4	0.0
	B	2–20	0.1	4.3	33.4	55.0	5.6	0.8	0.7	5.8	0.08	0.003	25.3	0.0
	B/C	20–30	0.0	0.6	8.6	79.4	10.8	0.2	0.4	5.7	0.08	0.003	23.3	0.0
	C[b]	50	0.1	7.7	38.6	48.9	3.6	0.1	1.0	5.9	0.02	0.001	15.9	0.0
	C	600	0.1	8.9	68.1	21.2	1.2	0.3	0.2	6.9	ND	ND	ND	0.0
3	C	50	0.1	3.8	38.7	45.8	9.7	1.7	0.2	6.5	ND	ND	ND	0.0
	C	600	0.2	11.0	24.0	54.8	8.6	1.1	0.3	8.1	ND	ND	ND	0.0
	C	1500	0.0	14.7	26.0	56.5	2.7	0.0	0.1	8.1	ND	ND	ND	0.0

[a] Bulk densities of the Ae horizon were 1.35 to 1.45.

[b] Bulk densities of the C horizon were 1.5 to 1.6.

Table 4. Saturated hydraulic conductivities of sand samples from the Richardson Fire site.

Site	Horizon	Conductivity cm/hr
1	C	40.1
2	Ae	43.5
	Bm	35.4
	C	31.3
3.	Ae	57.6
	C	26.6

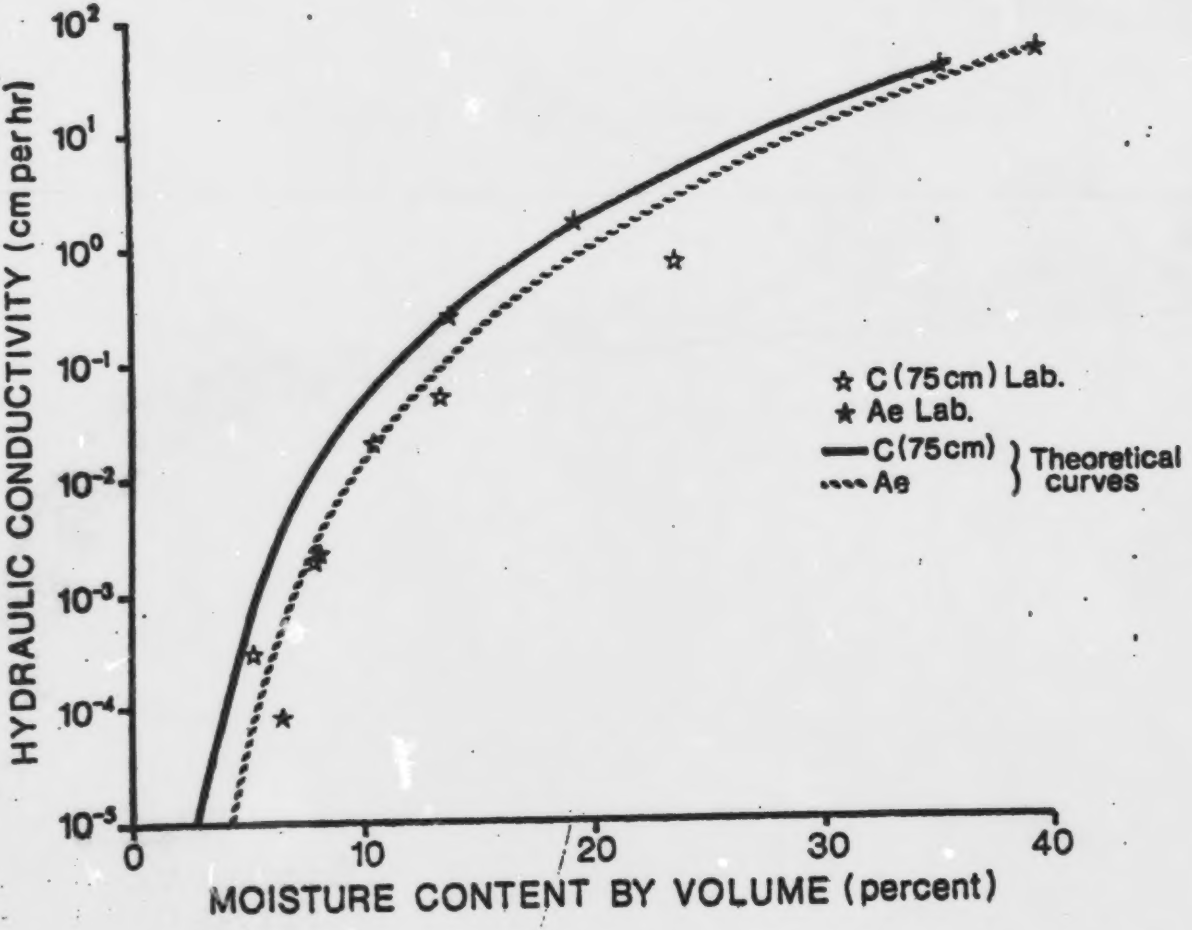

Figure 7. The relationship between hydraulic conductivity and soil moisture for two soil horizons at the Richardson site.

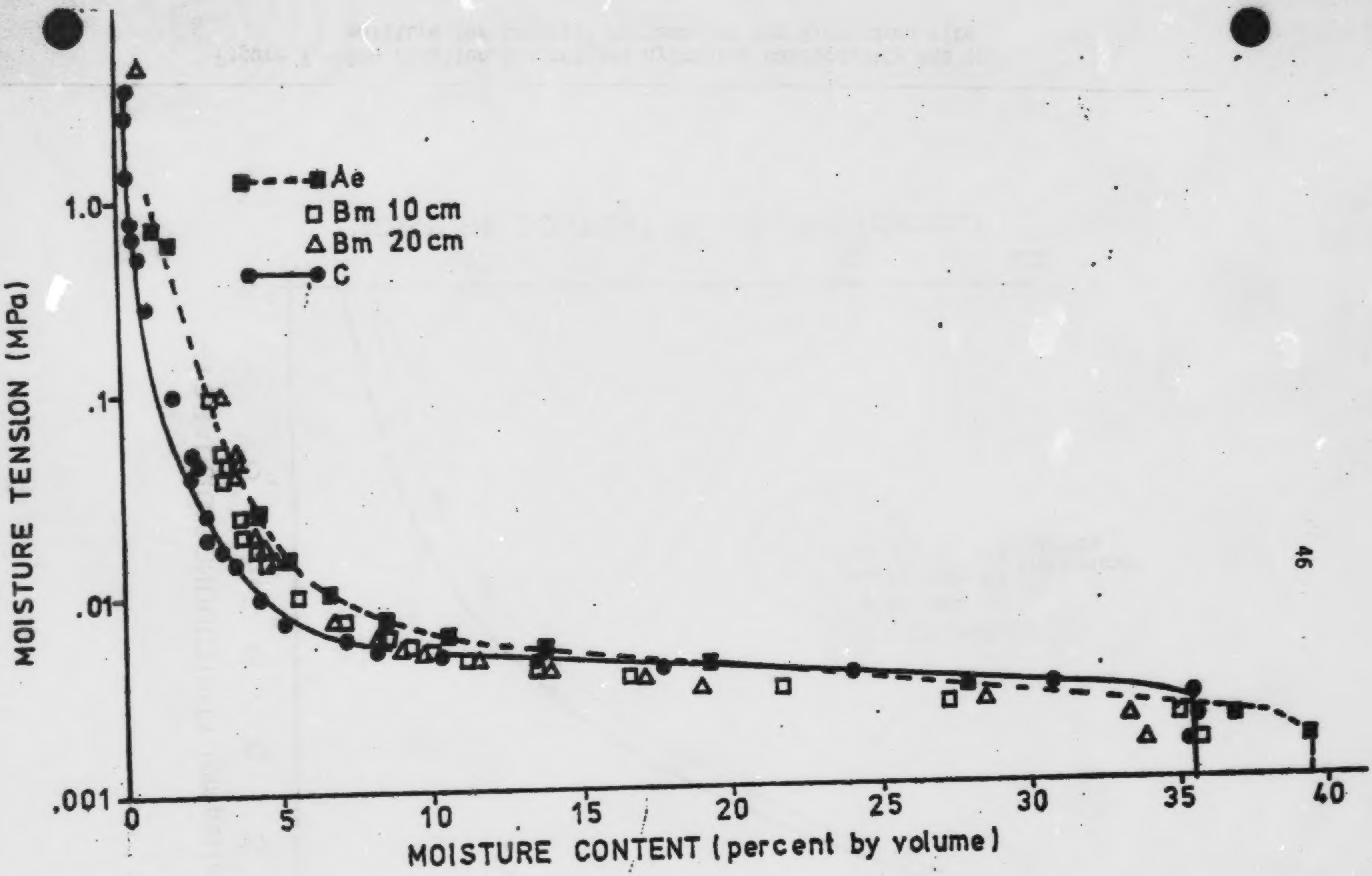

Figure 8. Moisture retention curves for different soil horizons at the Richardson site.

5.1.2 Field Studies

Seasonal soil temperatures at the three hillside study sites (Figure 2) are given in Figure 9. The 0°C isotherm, at the middle site, reached its deepest level early in April just at the time of thaw. Thawing was extremely rapid and was complete by early May. Rapid thawing is probably due to 1) the SW exposure of the hillside; 2) the low moisture holding capacity and consequent low heat capacity of the sand; and 3) the high saturated hydraulic conductivity, resulting in rapid meltwater infiltration. Soil temperatures were above 15°C from early June to mid-October and continuous freezing temperatures did not occur until early November. The middle site (Figure 9) was somewhat warmer than the other sites, presumably because it has a steeper (SW) slope than the lower site and is less shaded than the upper site.

Moisture content was obtained from a combination of neutron probe and gravimetric measurements. Results for the middle site (where the bulk of the physiologic measurements were made) are given in Figure 10. Moisture levels at 600 cm remained relatively constant over the study period. The other sites (Figure 2) were similar to the middle site except that site 1 (upper) generally had less moisture at 900 and 500 cm, presumably due to a few boulders in the profile.

The spring thaw period is of particular interest since a large amount of water is released during a short time period (3 or 4 days, in 1976) while soil temperatures are generally below 0°C. In 1976 the thaw meltout took place during the first few days in April with negligible surface run-off. It was obvious from gravimetric samples that the neutron probe gave erroneous values within 100 cm of the surface when there was a large difference between surface soil moisture content (30%) and that at depth which remained near 3-4%. Accordingly gravimetric values were used for the near surface samples and the neutron probe at depth. On April 3, the surface layers were saturated, by April 4 melt water was in the 0-50 cm layer and by April 7 the surface 50 cm had drained and most of the meltwater was in the 100-150 cm "bulge" (Figure 10) where soil temperature was -1 to 0°C. April 7 was taken as the base for water balance calculations. Particular attention was given to the thaw period in 1977 (Figure 10). As in 1976, no significant runoff was observed even though thaw was rapid. Comparisons of the amount of water in the snowpack with the amount in the soil after snow melt were made to see if in fact the water in the snow pack was moving vertically into the soil. At the middle site the two values agreed

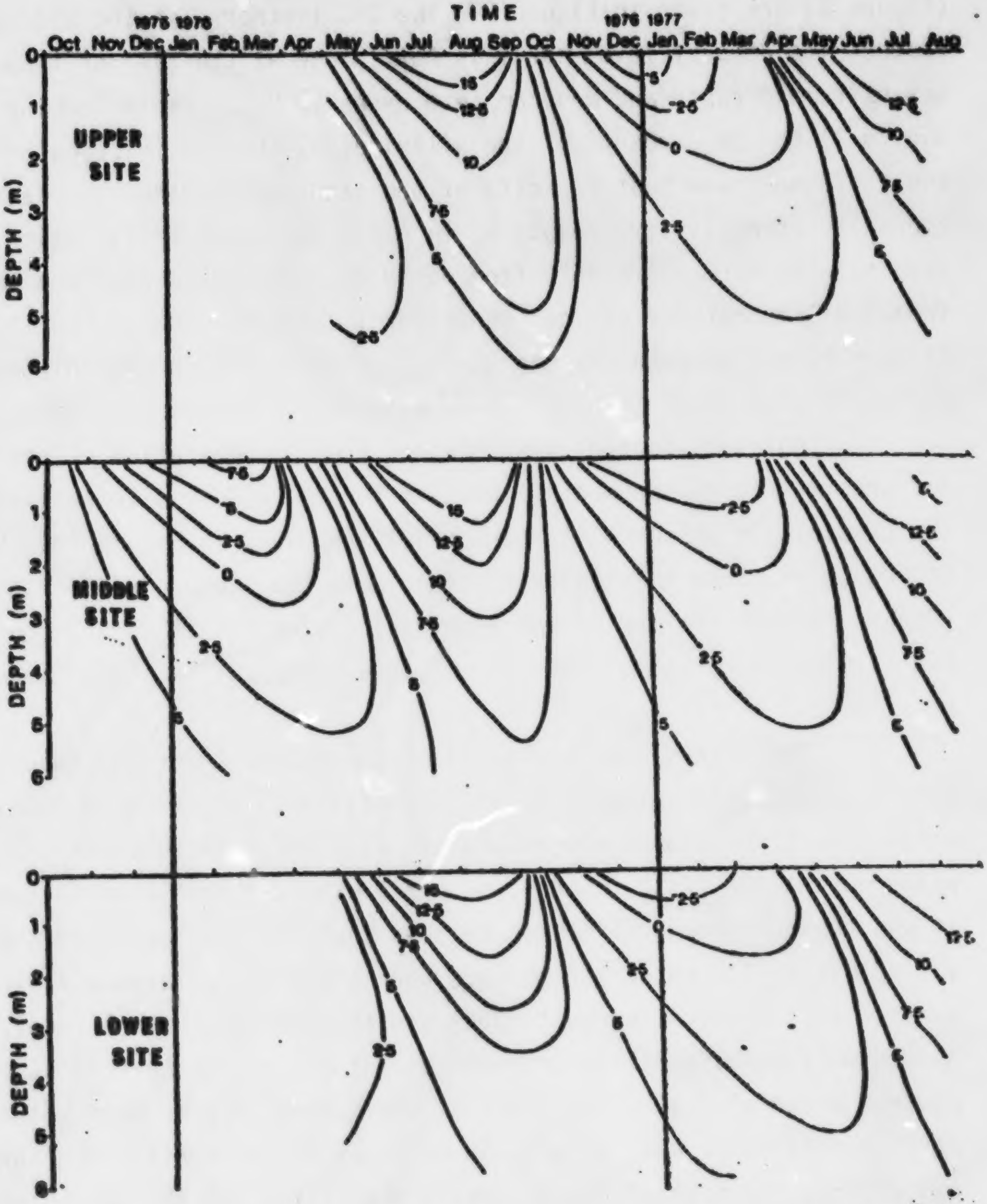

Figure 9. Richardson soil isotherms in relation to depth at the 3 hillside locations.

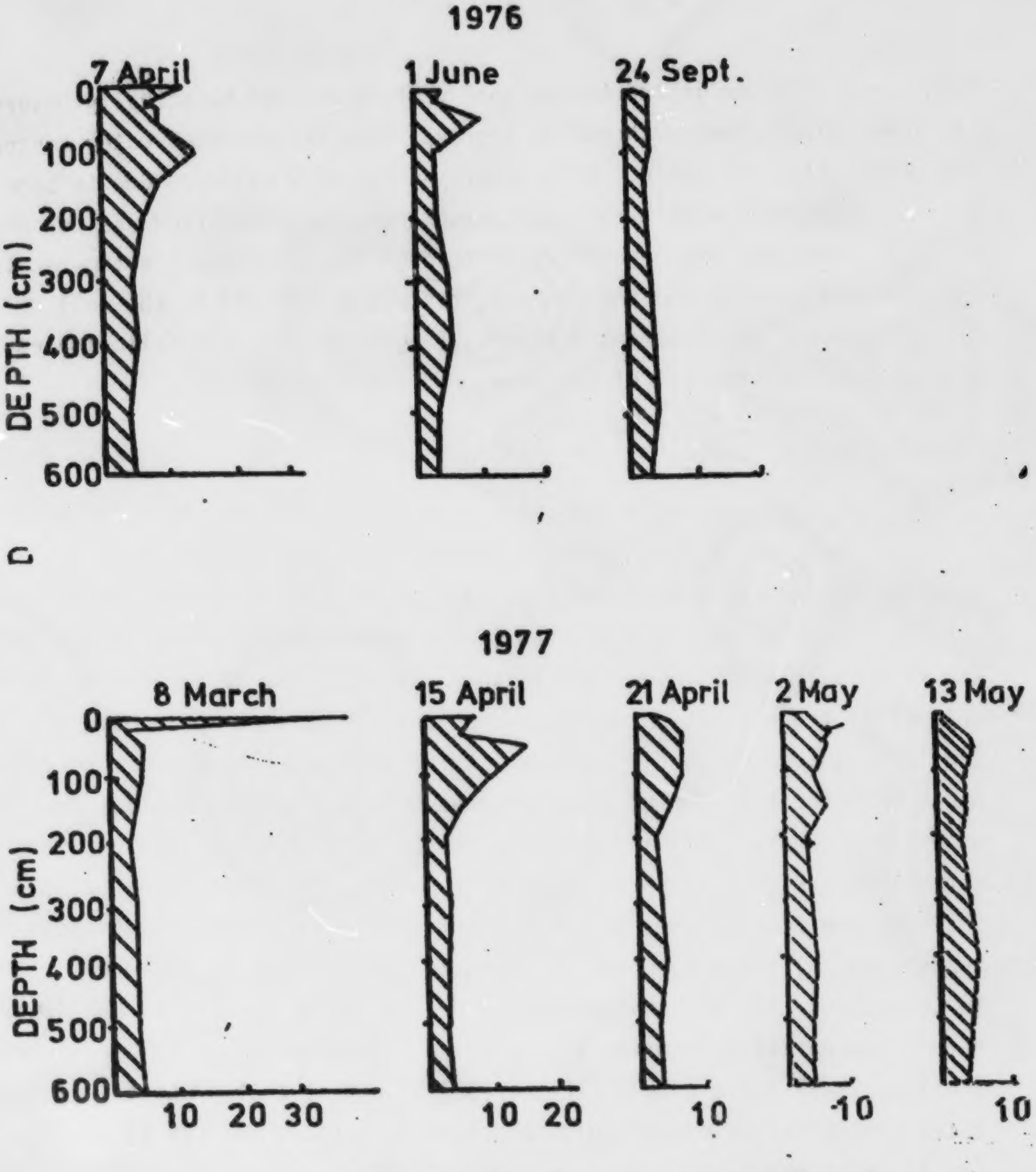

Figure 10. Middle study site soil water content profiles at selected dates during 1976 and 1977.

fairly well (315 mm in the 600 cm soil profile and 302 mm actually observed). The lower site actually showed an increase over the expected water content and the upper site a decrease. Both discrepancies were believed due to some lateral downslope movement within the soil, even though overland flow was not observed.

Vertical drainage of water through the profile was estimated in two ways: 1) during the thaw period this was determined by the well defined "bulge" of melt water moving downwards (Figure 10); 2) the following equation was used during the rest of the year:

$$D = \int_{t_1}^{t_2} (K_\theta + K_\theta {}^{\partial h}/_{\partial z}) \partial t$$

where: D = drainage; K_θ = hydraulic conductivity; h = suction in cm of water; z = depth; and t = time.

Drainage during these times were based upon the 250 cm measurements because at 250 cm both thermal and tension (water potential) gradients are small and relatively stable over long periods. Since K was determined at 75 cm (Figure 7) the assumption was made that the 250 cm sand would have a similarly shaped conductivity vs moisture curve and the values were adjusted based upon the thaw period of water movement (Rose et al. 1965). Cumulative water input, water loss and drainage for the 1976 and 1977 seasons were determined. Figure 11 shows the 1977 results. The differences between the drainage and total loss should represent tree and shrub uptake (mostly transpiration) since evaporation from the lichen layer is included in the calculation of non-intercepted precipitation and the lichen layer reduces evaporation from the soil surface. Cumulative water losses were similar at all three sites. These results suggest that 47 to 48% of the total precipitation drains below the root zone (i.e. 167 (yr 2) to 195 (yr 1) mm of water).

Soil moisture tensions (-water potential) were never very great. Tensiometers failed to give accurate readings for tensions greater than .01 to .02 MPa and psychrometers were often erratic near the surface. However the tensiometers, psychrometers and moisture release curve (Figure 8) provide evidence that the soil was never very dry. The highest tension measured was 1.8 mPa at 10 cm on 12 May, 1976 but at 20 cm the tension was < 0.1 MPa. It is obvious from the soil moisture data (Figure 10) and the

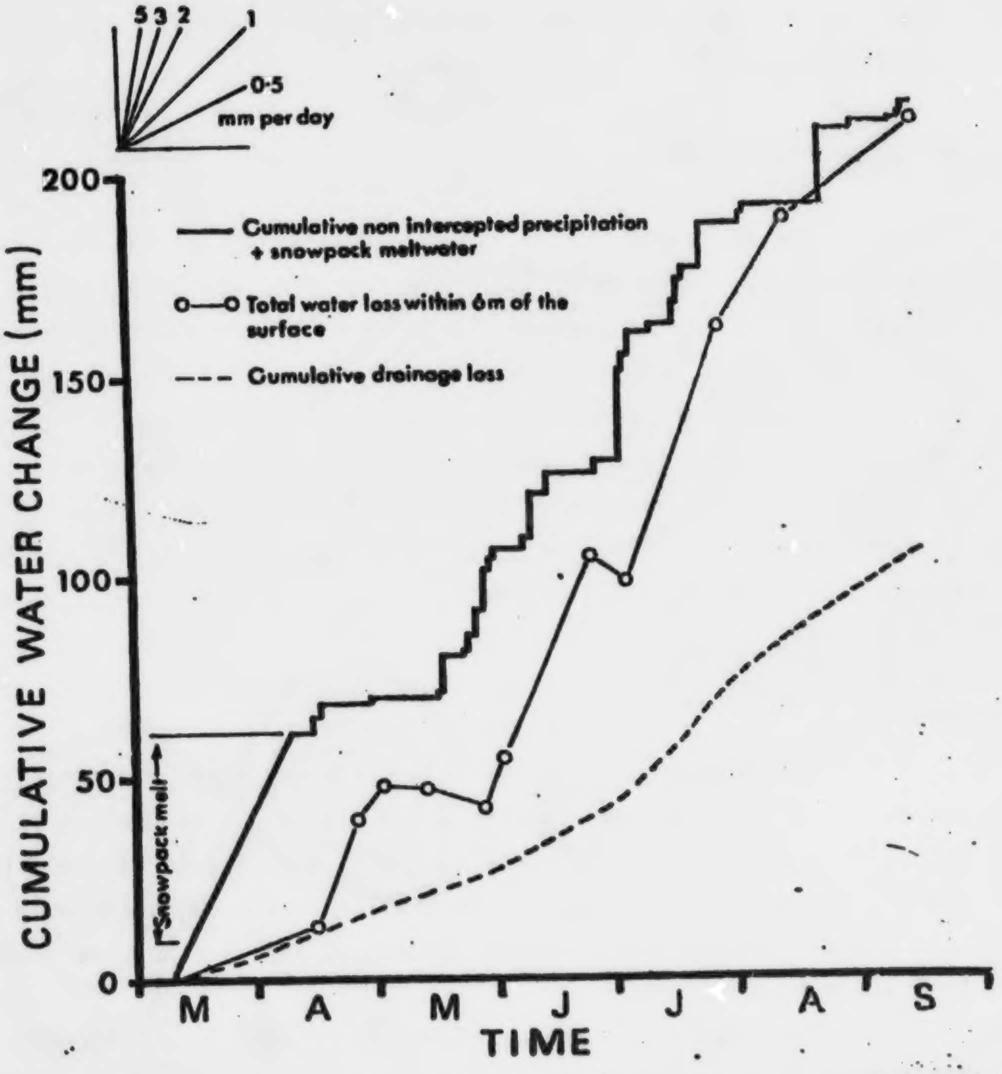

Figure 11. Cumulative total water loss within 6 m of the soil surface during 1977 growing season at the middle site compared with non-intercepted precipitation.

moisture release curve (Figure 8) that tensions were generally low indicating little if any soil moisture stress during the two study seasons. This is born out by the Jack pine xylem tensions (Figure 23) which also prove the trees were well watered.

The absolute level in the water table wells varied very little supporting the assumption that the hill does not contain a core of slowly permeable material.

5.2 METEOROLOGY

5.2.1 1976-1977 Weather

The global shortwave radiation regime was similar for the two years (Table 5). Mean daily shortwave radiation was very similar for May-July during the two years. The greatest observed difference was for August with 1976 receiving 50 $W\ m^{-2}$ more than in 1977.

The percentage of diffuse radiation to incoming shortwave radiation was consistently greater in 1977 because of the higher amounts of cloud cover that field season; the differences ranged from only 1.5% in June, which is usually the month of maximum precipitation, to 20% in August. Longwave incoming radiation values also showed consistently higher fluxes in 1977, again due to cloud cover. With overcast sky conditions, the sky radiant temperature is higher and therefore the amount of emitted longwave thermal energy is greater.

Net radiation values are the differences between incoming and outgoing radiation and therefore are strongly dependent on the radiative properties of the surface. Since the surface did not change, the net radiation values were quite similar in May, June and July in both years. Net radiation values for August 1977 are not available due to instrument problems.

The temperature regime (Table 5) depends to a large extent on the radiation regime. The mean monthly temperatures for both years in May were almost the same (13.8 vs 13.7°C). June and July of 1977 were approximately 1°C cooler than in 1976 a further indication of the greater amount of clouds in 1977. August 1977 was cooler by more than 4°C than August 1976 which is not surprising since the incoming radiation was lower by 21% in August 1977 from the previous year.

Table 5. Richardson monthly climatic summary (1976, 1977).

Parameter		MAY	JUNE	JULY	AUG.	Total
Mean daily shortwave radiation (Wm^{-2})	1976	216	213	194	229	
	1977	200	229	204	180	
Mean daily diffuse radiation (% incoming)	1976	34	39	37	23	
	1977	40	40	40	44	
Mean daily longwave radiation (Wm^{-2})	1976	323	335	391	288	
	1977	391	432	427	404	
Mean daily net radiation (Wm^{-2})	1976	156	177	151	190	
	1977	154	176	163	M	
Temperature (°C)	1976	13.8	17.3	17.5	17.6	
	1977	13.7	16.2	16.2	13.4	
Wind speed (ms^{-1})	1976	1.96	1.91	1.76	1.59	
	1977	1.62	1.77	1.49	1.65	
Total precipitation (mm)	1976	22.3	71.9	67.7	33.3	195.2
	1977	57.7	43.2	85.4	46.0	232.3

The precipitation values (Table 5) reveal substantial month-to-month and year-to-year variability. On a total basis for both field seasons, 1977 had 28 mm of rain more than 1976, while on a month-to-month basis May, July and August had more precipitation in 1977 while only June had less precipitation in 1977 than 1976.

Mean wind speeds (Table 5) were quite low in all months with a range from 1.5 to 2.0 ms^{-1}. Average speeds for the four-month field season were slighly lower in 1977 than in 1976.

Daily climatic information was gathered both field seasons and is reported in detail in the 1977 and 1979 reports. Data presented here are given to illustrate certain points. Total incoming solar radiation (global-direct and diffuse-indirect) varied seasonally from mean daily values of 110-140 W m^{-2} in March, there was a gradual increase to a peak of 300-330 W min June, and then a slow decrease after solstice to 200 W m^{-2} in early to mid-August (Figure 12). Values decreased to 125 in September, 75 in October and 25 W m^{-2} in early December. Diffuse radiation did not vary as much as the direct + diffuse (i.e., total) radiation components. Diffuse radiation varied from a mean of 60 W m^{-2} in March to 80-90 W m^{-2} in May and June. The lower values in the early part of the season resulted from the drier Arctic air masses, shorter day lengths, and low sun angles of early spring. On the average, diffuse radiation was found to be 40% of the total incoming shortwave radiation. However, during the passages of low pressure systems accompanied by the corresponding cloud patterns, diffuse radiation was almost 100% of the total incoming radiation. Examples of this occurred in early April, mid-May, end of May, early July, and mid-July, 1977.

Figure 13 illustrates the two main components of radiation, namely, all-wave incoming (shortwave plus longwave) and all-wave outgoing radiation. All-wave incoming radiation was very similar to the global shortwave radiation previously discussed. The all-wave outgoing radiation was much smaller and less variable because it is controlled by the surface and is not sensitive to cloudiness. The area between the two curves is the net or absorbed radiation. Net radiation values started to 70 W m^{-2} in early March, increased to 145 W m^{-2} in mid-April, 180 W m^{-2} in mid-May and reached a mean maximum of 207 W m^{-2} in mid-June followed by a gradual decline.

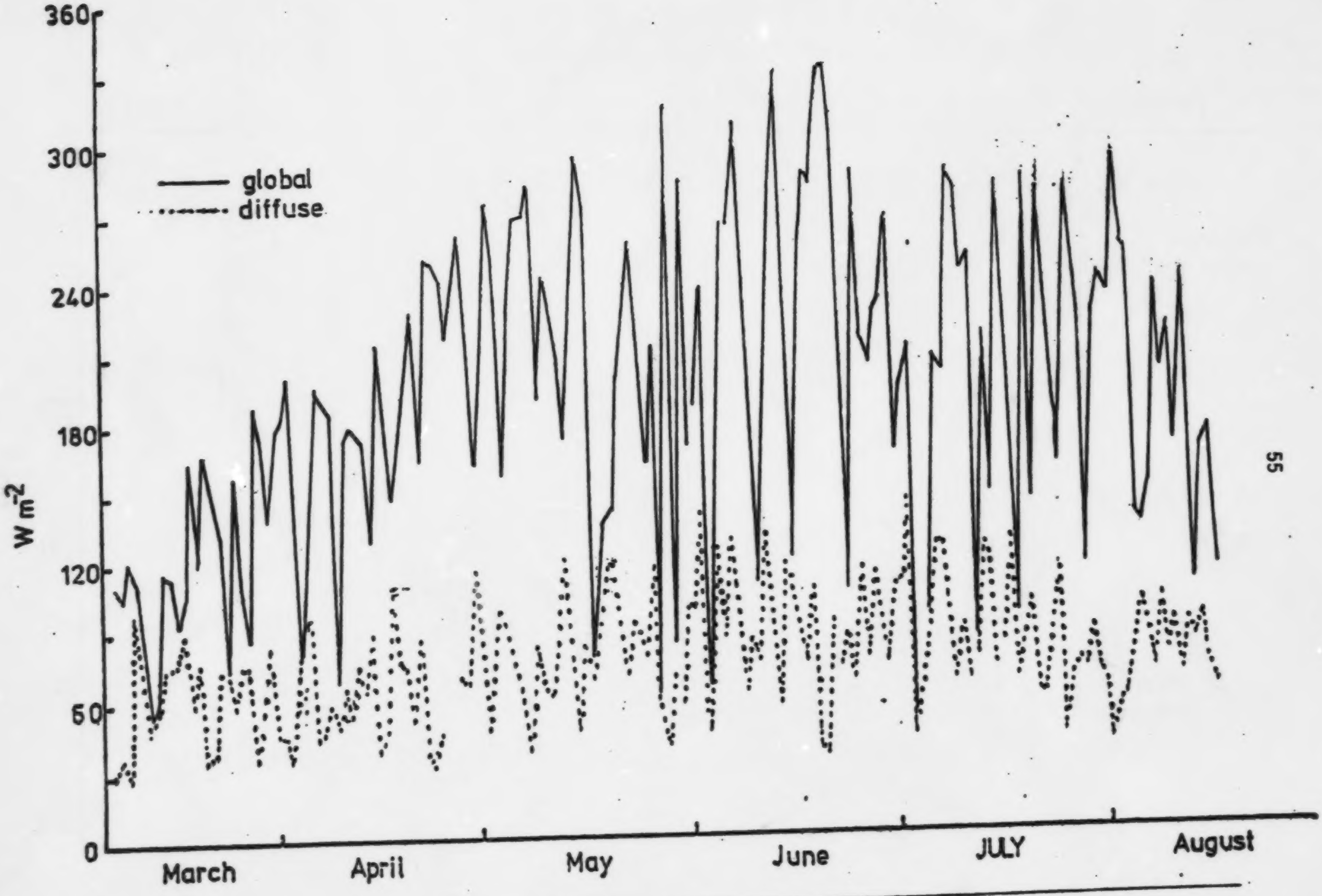

Figure 12. Mean daily global incoming direct and diffuse radiation during 1977.

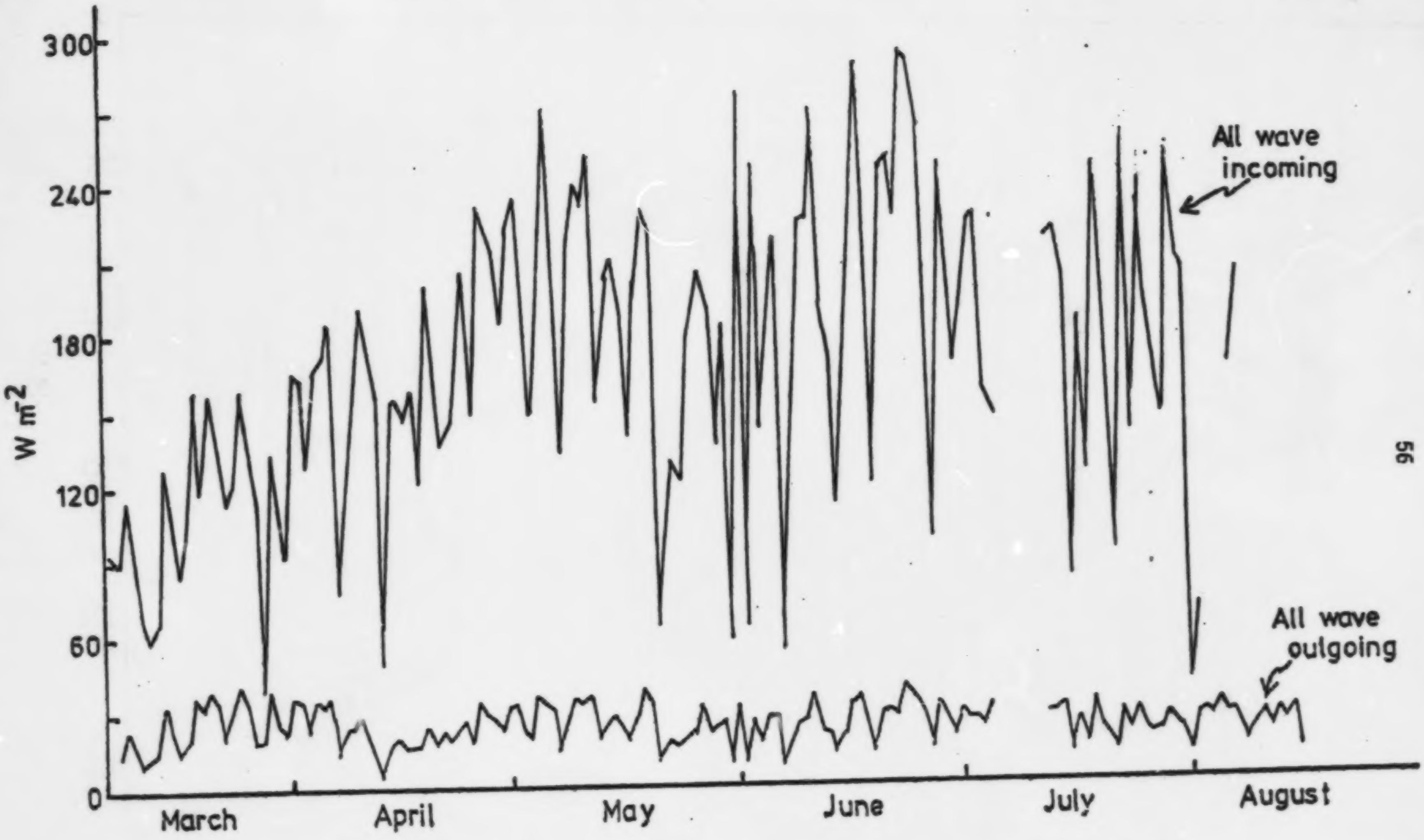

Figure 12. Mean daily incoming and outgoing all wave (300-6000nm) radiation.

Photosynthetically-active radiation (PhAR) (400-700 nm) is one of the most important components of radiation which can be measured in a plant process study. The energy available in the range of PhAR is usually 50% of the incoming solar radiation (Galoux 1971). From mid-April to early May 1977 the mean daily value was 400 $\mu Em^{-2}\ s^{-1}$. Mean values then increased to 500 $\mu Em^{-2}\ s^{-1}$ in mid-June, and then decreased to 300-400 $\mu Em^{-2}\ s^{-1}$ by mid-July. As expected, PhAR exhibited the same seasonal pattern and day-to-day variations as solar incoming radiation because its wavelength range is well within that of the solar radiation.

Daily mean air temperature was plotted for three sites which represent a transect from the bottom of the hill, through the mid-slope main tower site and further to the upper slope near the top of our plot distribution. The temperature differences between the sites will be discussed later and only the general seasonal trends will be looked at now.

The field season started in early March with unusually high temperatures (Figure 14). For the first few days of measurement the mean daily temperatures were above freezing. This was followed by a fresh outbreak of cold Arctic air which brought temperatures to near -20°C. After this initial cold spell a gradual increase of temperature can be observed but with irregular additional outbreaks of cold air on March 28, April 1, and April 2. Temperatures rose above the freezing level premanently on April 5 as the general seasonal warming continued. The highest mean daily temperature was reached on June 20 (24.9°C) preceded by several outbreaks of cool air from the north. Following the maximum temperature in mid-June there was a cool period from July 11 to July 19. From July 19 to early August the temperatures were again seasonal (18°C) followed by cooler temperatures till the end of the field season.

5.2.2 Soil Temperature and Soil Heat Flux

Soil temperatures for the 1977 season have a similar shape but smaller amplitudes than air temperature (compare Figs. 9 & 14). The near surface (-2, -8 cm depths) soil temperatures track air temperatures and from May through July are generally within 3 to 5°C of each other. Temperature pattern at -200 cm is very different, remaining near freezing

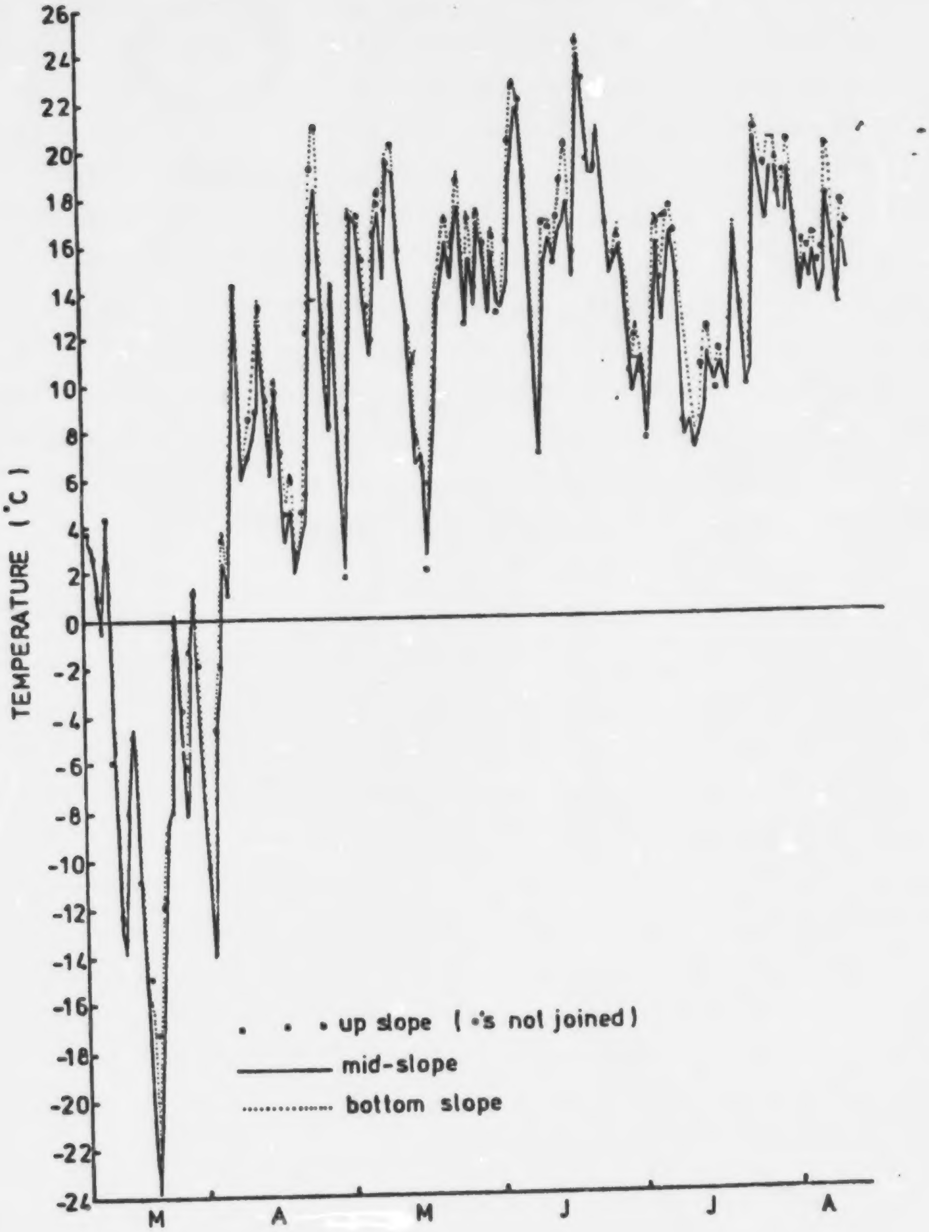

Figure 14. Mean daily air temperatures for the 3 hillside meteorological sites at Richardson.

until mid-May then warming rapidly until early July, followed by a second peak in August. Maximum temperatures at this depth were generally 8 to 12°C lower than near surface soils and with a 3-4 day lag.

Soil heat flux is only a small fraction of absorbed net radiation, especially under tree canopies. Over the March-August measurement period, soil heat flux was 7% of the net radiation received just above the canopy and 10-15% of absorbed energy measured above the forest floor under the canopy. This seeming increase in percent absorbed by the soil results from a much smaller amount of net radiation received at the forest floor vs above the tree canopy. In spring there was a net outflow of heat from the soil with lower air temperatures. With the onset of snow melt, soil heat flux became positive and varied from 2-18 W m^{-2} the rest of the measurement period.

5.2.3 Wind

The exchange of water vapour, carbon dioxide, heat and momentum between a canopy and the bulk air above it, depend upon the turbulent exchange properties of the wind profile generated in the boundary layer above the canopy (Jarvis et al. 1976). Winds at Richardson were very light, averaging ≈1.5-1.8 m s^{-1} the two summers above the canopy at 8 m. Mean daily winds ranged from minima of 0.4-0.6 m s^{-1} to maxima of 3.0 to 5.2 m s^{-1} . Mean daily wind values varied from 2.0 m s^{-1} in May and June down to 1.5 m s^{-1} in July and August, back to 2.0 m s^{-1} in September and October in 1976. In 1977 mean daily winds were 1.5 m s^{-1} March to mid-April, 2.5 m s^{-1} in mid-April to mid-May, and about 1.5 m s^{-1} mid-May through August.

5.2.4 Precipitation and Interception

Precipitation was light early in the season both years, reaching a peak in July or August (Figure 15). The 1976 field season was near normal and 1977 above normal compared with the long term records.

Snow cover was average in early March, 1977, (32 cm) on the hillslope. Snow cover increased to 47 cm the third week of March, then steadily declined from 28 cm on 8 April to 18 cm on 9 April and was completely melted by 11 April. The entire area was snow-free by 15 April, except for sheltered snow patches.

Summer precipitation is generally of low intensity (10.5 mm h^{-1}); though two "cloud bursts" in 1977 resulted in high intensity rainfall (July

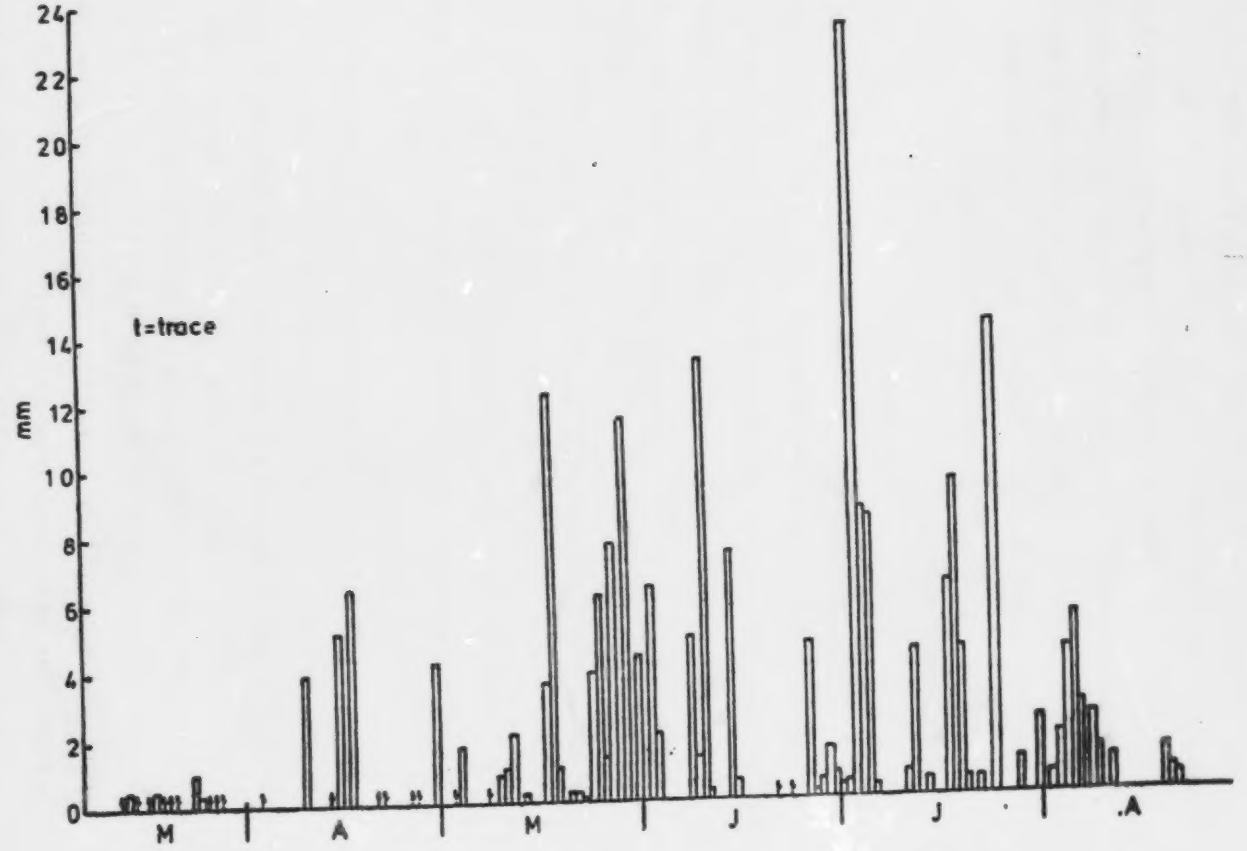

Figure 15. Total daily precipitation for the 1977 field season.

5, 17.8 mm h^{-1}, July 24, 28.4 mm h^{-1}). In 1977 the frequency of precipitation was quite high (Figure 15) with no extended dry periods.

The use of throughfall collectors within the forest permitted the calculation of percent canopy interception in relation to total precipitation. With light showers of 1-3 mm, 70-95% of the rain is intercepted. For all storms in 1977, mean interception was 30%. This compares reasonably well with an average 21% interception in a 50 yr Jack pine stand (Mitchel 1930). Based upon observations, branch flow and drip were more important than trunk flow. Stemflow results are not presented because of unreliable data, but other studies indicate this averages 1-16% of total precipitation, depending upon storm size (Kittredge 1948).

5.2.5 Selection of a dry season for modelling

All available climatic data for the oil sands region were analyzed to find typical dry conditions. The 5 mon period, April to August was chosen as the growing season. The previous winter, September to March, was also considered in determining a hot-dry season. Appendix A in the 1977 Report (Hage et al.) summarizes the data and selects 1953 as typical hot-dry growing season.

5.3 MYCORRHIZAE

5.3.1 Mycorrhizal Fungi Associated with Jack pine

The ectomycorrhizal fungi that have been collected at the Richardson site are listed in Appendix 2 (1979 report). If more than one potential host was present, the host plant could not be determined. Many of the species remain to be identified but 57 species were collected that are considered symbionts of Jack pine. Many or most of these may also be associated with bearberry as typical mycorrhizal fungi of pine have been shown to form ectendomycorrhizae with bearberry (Zak 1976a). Four species of hydnums are included in this list although hydnums are not included in the list of mycorrhizal fungi by Trappe (1962). The circumstantial evidence that they may be mycorrhizal include the consistant association with certain forest types and the failure to grow in culture (Harrison 1971).

The most common sporocarps observed on the site were those of *Suillus tomentosus* and *Russula* spp. The abundance of fruiting bodies is usually not considered an indicator of the importance of a particular species as a symbiont (Riffle, 1973). However Laiho (1970) found a significant positive correlation between the number of sporophores of *Paxillus involutus* and the number of mycorrhizae formed by *P. involutus* in mixed forest stands.

In order to determine if the fungi associated with Jack pine were similar under different environmental conditions, observations and collections were made on four areas.

Fruiting was rare in the burn area thus limiting the possible comparisons with the other sides but sporocarps were common on the more protected roadsides. Observations on the sporocarps on the disturbed and natural areas suggests that different fungi form mycorrhizae with pine on natural and disturbed soils (Table 6). Caution is in order however when interpreting observations on sporocarps as their absence may be due to unfavorable conditions for fruiting and the fungi may be present and active in a vegetative state. The genus *Russula* is not included as species could not be determined in the field. Distinct preferences for fruiting in natural stands were noted for *Elaphomyces* spp., hydnums, *Suillus* spp. and several agarics. *Elaphomyces granulatus* was found in the driest Jack pine stands with a *Cladina* lichen carpet, whereas *E. muricatus* was always found in mixed stands of pine, often with a deep cover of feather mosses, in association with hardwood species (e.g. green alder, paper birch, aspen).

In 1975 *Laccaria laccata* was very abundant along roads and among bearberry in the airstrip. In 1976 conditions were less favorable for fruiting and it was rarely encountered. Considering the reputation of this species as a "weed" and its very wide distribution (Miller 1962), it may be significant that it was not found in mature stands. Laiho (1970) found that *L. laccata* and *Thelephora terrestris* increased in abundance in cutover areas a compared to closed stands. Although these two species are adapted to disturbed soils in the Richardson area they may not be desirable mycorrhizal associates. Both are common in forest nurseries (Hacskaylo 1965, Stack et al. 1975) but they may be relatively ineffective symbionts (Mikalo 1970). Inoculation of planting stock with more effective fungi may be desirable on nutrient poor, excessively drained soils.

Astraeus hygrometricus and *Scleroderma meridionale* were conspicuous components of the fungal flora in disturbed soils in exposed locations. Their importance is likely to be overestimated in that the tough gastrocarps persist on the soil and can overwinter in place. In contrast, the agaric

Table 6. Distribution of sporocarps of the most common mycorrhizal fungi on natural and disturbed sites in the Richardson Fire Tower area.

Species	Area where found			
	Richardson slope	Other mature pine stands	Bare sand by roadsides	1970 burn
Elaphomyces granulatus	+[*]	+	-	-
E. muricatus	-	+	-	-
Hydnellum peckii	+	+	-	-
Hydnum imbricatum	+	+	-	-
Bankera fuligineo-alba	+	-	-	-
Phellodon melaleucus	-	+	-	-
Cantharellus cibarius	-	+	-	-
Suillus tomentosus	+	+	(+)	-
Suillus sp. 2	+	+	-	-
Armillaria ponderosa	+	-	-	-
Chroogomphus rutilis	+	+	-	-
Cortinarius ?semisanguinensis	+	-	-	-
Cortinarius sp. 1719	+	-	-	-
Astraeus hygrometricus	-	(+)	+	+
Scleroderma meridionale	-	-	+	+
Thelephora terrestris	-	-	+	-
Rhizopogon rubescens	(+)	-	+	+
Lactarius sp. 2191	(+)	-	+	+
Laccaria laccata	-	-	+	+
Tricholoma flavovirens	(+)	(+)	+	+
Hygrophorus sp. 2478	-	+	+	-

[*] + = present, - = absent, (+) = present but rare in comparison with the other areas where found.

species are rapidly riddled by insects and are short lived.

The spores of *Scleroderma* and *Astraeus* could possibly be used to inoculate seedlings as the gastrocarps are easily recognized and collected. Observations indicate that the best time to collect *Astraeus* gastrocarps for spore inoculum is in the fall. Spores collected from fruit bodies of another gastromycete, *Pisolithus tinctorius*, have been used successfully to inoculate loblolly pine in the southeastern U.S. (Marx 1976). The fruit bodies of *Astraeus* are much smaller than *P. tinctorius* and a very large number would be required for inoculating large numbers of trees.

Rhizopogon rubescens was the most common hypogeous fungus at Richardson and was always found along roadsides except one find at the border of the plots. A few immature specimens were found on 20 June, a few mature specimens in mid-August and abundant mature basidiocarps in late September. It was also associated with lodgepole pine in central Alberta in August. The preference for fruiting on bare or disturbed soils is not a characteristic of the species but it is a complex and widespread species with many variants (Smith & Smith 1973). Species of *Rhizopogon* have frequently been used in synthesis studies with pine (Trappe 1962).

5.3.2 Direct Isolation of Symbionts from Mycorrhizae

Populations of ectomycorrhizal fungi on the Richardson slope and the 1970 burn were compared by examining fungi cultured from surface sterilized mycorrhizae. It is inherent in the method that only a portion of the mycorrhizal fungi will be detected as many will not grow in culture. However the importance of those fungi that do grow in culture can be more accurately assayed than by observations on fruit body abundance.

The rate of recovery of possible symbionts indicate that the surface sterilization - medium combination was a successful method for isolating ectomycorrhizal fungi. The addition of benomyl to the MMN medium increased the rate of recovery from 9.5 to 32.2% on a separate isolation experiment with 1300 root tips. The recovery of possible symbionts from the slope and burn was 36 and 20% respectively. The difference in recovery rate from the two areas was largely due to the presence of very slow growing hyaline species on the slope which were largely absent on the burn.

Table 7. Species of mycorrhizal fungi isolated from two or more samples at either site by surface sterilization of mycorrhizal root tips.

Species or Group	Slope Site Percent of Samples	Slope Site Number of Tips	Burned Area Percent of Samples	Burned Area Number of Tips
Astraeus hygrometricus	0	0	8	16
Lactarius sp. 1	4	6	21	76
Lactarius sp. 2	3	13	3	5
Rhizopogon rubescens	3	4	4	5
Suillus tomentosus	4	8	0	0
Suillus sp. 2	4	9	15	29
Tricholoma sp. 2488	5	19	0	0
Tricholoma sp. 2	12	41	0	0
Tricholoma sp. 3	2	3	7	12
Tricholoma sp. 4	8	12	0	0
Tricholoma sp. 5	3	6	0	0
Species no. 11	45	130	3	2
Species no. 22	15	42	0	0
Species no. 38	7	11	1	1
Species no. 13	4	8	0	0
Species no. 58	4	4	0	0
Species no. 47	3	7	0	0
Species no. 16	3	6	3	8
Species no. 91	3	5	0	0
Species no. 82	2	5	0	0
Species no. 40	2	4	0	0
Species no. 12	2	3	0	0
Species no. 45	2	3	0	0
Species no. 48	2	3	0	0
Species no. 51	2	3	0	0
Species no. 39	2	2	0	0
Species no. 85	2	2	0	0
Species no. 14	0	0	12	28
Species no. 17	1	2	5	6
Species no. 19	0	0	4	13
Species no. 32	0	0	4	11
Species no. 27	0	0	3	3
Species no. 80	1	1	3	3

The fungi isolated from the mycorrhizae were placed in 82 species groups (Table 7). Of these 82 groups, 49 were found in only one sample on either the slope, the burn or both. Sixteen percent of the 82 species were found on both areas, 23% exclusively on the burn and 61% only on the slope. The species diversity was almost twice as great on the slope as on the burn (62 vs 32 species). The total number of species is very large, especially considering that only one-fifth to one-third of the mycorrhizae yielded viable cultures.

Only a small percentage of the isolates could be matched up with isolates from fruit bodies or placed in generic groups. The 11 taxa that were recognized accounted for 32% of the isolates but only 9% of the total root tips plated.

Astaeus hygrometricus was isolated exclusively from the burn and *Lactarius* sp. 1 and *Suillus* sp. 2 were more abundant in the burn than on the slope. *Tricholoma* species were more common on the slope and *Suillus tomentosus* (based on only 8 isolates) was confined to the slope. The two most common species isolated from the slope could not be identified (numbers 11 and 22). Of the species that were commonly isolated, it appeared that they occurred at a low frequency over the entire area sampled. Species Number 11 was found in 45 samples on both slope transects with no obvious clustering. Of the possible 15 tips per sample, it occurred on one tip 23 times, two 24 times, three 12 times and four to six 5 times, showing a general rather than clustered occurrence. Data for the other species, where sufficient, indicates similar distribution patterns.

5.3.3 Identification and Abundance of Specific Mycorrhizal Types

Visual estimates of the occurrence and abundance of several distinctive types of mycorrhizae were made on the soil core and seedling samples from the slope and burn. These included mycorrhizae formed by *Cenococcum graniforme* and *Suillus tomentosus* and vinaceous and green types. The *S. tomentosus* type was a dense cluster of dicotomously branched tips enclosed in a felt-like outer mantle of pale brown or vinaceous tinted mycelium. Cultures obtained from this subtuberculate type matched cultures from *S. tomentosus* basidiocarps. The green type may be formed by a species of *Lactarius* as cultures of *Lactarius* sp. 1 developed erect hyphal aggregations of green hyphae. Synthesis studies were conducted with *Lactarius* sp. 1. Green rhizomorphs were attached to the green mycorrhizae and were often fused to suberized roots. The green pismentation was erratic and abruptly disappeared giving rhizomorphs that were either hyaline or green.

Two of the seven specific mycorrhizae types which yielded cultures of *Lactarius* sp. 1 were green. The inconsistent occurrence of green pigmentation would result in an underestimate of the abundance of this type. The vinaceous type was distinctive due to the colour and the abundance of radiating vinaceous mycelial strands. This type could not be cultured by direct isolation techniques.

The occurrence of the mycorrhizae types showed distinct site preferences. *Cenococcum* was common in both the slope and burn, while the *Suillus* and vinaceous types were largely restricted to the mature pine stand. Green mycorrhizae were infrequently observed and green rhizomorphs were most common on the burn. These results are in agreement with the distribution of basidiocarps of *Suillus tomentosus* and *Lactarius* sp. 1 (Table 6) and the direct isolation data (Table 8).

Cenococcum was widely distributed but it was usually present as only a small fraction of the total mycorrhizae (Table 9). The *Suillus* type rarely constituted more than 5% of the total. As *Suillus tomentosus* was the most common mycorrhizal fungus fruiting in mature pine stands, these data show the lack of a quantitative correlation between sporocarps and mycorrhizae abundance.

Direct isolations were attempted from distinctive types of mycorrhizae in October 1975 and April and June 1976 in order to try to link specific fungi was mycorrhizae types. Isolates derived from the mycorrhizae were compared with isolates from basidiocarps. Basidiomycetes and a few hypogeous ascomycetes were collected from the Richardson site and lodgepole pine stands in central Alberta. The fungi were isolated by breaking the fruit bodies and plating small pieces of the context or peridium and hymenial tissues on MMN and MMN + benomyl media. Of the 38 taxa in which isolations were attempted from the Richardson site, 19 grew in culture. Notable among those that did not grow were the hydnums, *Cantharellus cibarius*, *Chroogomphus rutilis*, *Hygrophorus* sp. and several species of *Russula*. With the exception of the hydnums, all of these species are generally assumed to be mycorrhizal associates (Trappe 1962). The observation that less than half

Table 8. Occurrence of specific mycorrhizal types in core and seedling samples in June 1976.

Area	Total Number of Samples	Number of Samples Each Type Occurred In				
		Cenococcum	*Suillus*	Vinaceous	Green	Green Rhizomorphs
Slope transects	100	96	45	21	2	2
Burn - transect	50	41	0	0	4	17
Burn - seedlings	25	23	1	0	3	ND

Table 9. Visual estimates of *Cenococcum graniforme* and *Suillus tomentosus* mycorrhizae in core and seedling samples as a percentage of the total mycorrhizae.

Site	Total Samples	Percent Abundance Classes				
		0	<1	1-5	5-30	30
		Cenococcum - Number of samples in each abundance class				
Slope transects	100	6	56	27	8	2
Burn - transect	50	9	23	9	8	0
Burn - seedlings	25	2	17	5	1	0
		Suillus - Number of samples in each abundance class				
Slope transects	100	55	26	13	5	0
Burn - transect	50	50	0	0	0	0
Burn - seedlings	25	24	1	0	0	0

of the presumed mycorrhizal associates would grow in culture compares fairly well with the maximum 36% rcovery from root tips.

5.3.4.1 Pure culture synthesis of Jack pine mycorrhizae Fourteen species of fungi successfully formed mycorrhizae with jack pine in synthesis flasks. All but two of these were native to the Richardson area. One of these was an isolate of *Pisolithus tinctorius* from a southern pine donated by D. H. Marx. The other was an isolate from lodgepole pine in the Kananaskis region of Alberta. It is unusual in that it forms ectendomycorrhizae. Its identity is unknown although the absence of clamp connections on the hyphae and an intolerance to benolate suggests it might be an ascomycete.

In addition to those combinations listed here *Suillus sibericus*, *Tricholoma zelleri* and *Cenococcum graniforme* also formed typical ectomycorrhizae with jack pine in synthesis flasks. All the flasks inoculated with *Hydnellum* and *Elaphomyces* were contaminated and mycorrhizae were not formed. At the termination of the experimental period, thousands of spores of *Elaphomyces* could be seen in contact with the pine roots with no evidence of germination. Descriptions of the mycorrhizae formed by the other fungi are given in the 1979 report. The following fungi formed mycorrhizal associations with Jack pine and are described in detail in the 1979 AOSERP report: *Astraceus hygrometricus*, *Tricholoma flavovirens*, *Tricholoma pessundatum*, *Suillus tomentosus*, *Scleroderma macrorhizon*, *Pisolithus tinctorius*, *Lactarius chelidonium*, *Laccaria laccata*, *Bankera fuligineo-alba*, and *Coltrichia perennis*.

A limited number of bearberry mycorrhizal symbionts were also tested. All of the fungi formed ectomycorrhizae with Jack pine as well. All of the fungi tested formed ectendomycorrhizal infections. The following fungi formed mycorrhizal associations with bearberry (*Arctostaphylos uva-ursi*): *Astraeus hygrometricus*, *Coltrichia perennis*, *Lactarius chelidonium*, *Rhizopogon rubescens*, *Tricholoma flavovirens*, and *Suillus sihiricus*. These are fully described in our 1979 AOSERP report.

5.3.4.2 Synthesis of mycorrhizal with Jack Pine and Isolates from surface sterilized mycorrhizal. Results of this experiment showed that surface sterilization of mycorrhizae with H_2O_2 and plating on a benolate amended medium was highly selective for mycorrhizal symbionts.

Sixteen of the 18 ramdomly chosen isolates formed ectomycorrhizae with pine in the vermiculite-peat substrate. This indicates that a majority (89%) of the 82 species groups truely represented mycorrhizal fungi. Of the two that failed to infect the roots one was very slow growing and one very rapid. Three of the random isolates could be matched with isolates from basiciocarps and formed mycorrhizae typical for the respective species. Five of the 18 species formed mycelial strands in the synthesis tubes thus not indicating a strong selective pressure for this morphological feature. Only four of 16 mycorrhizal types were distinctive enough in morphology and colour to permit identification in the field. These included two unknowns, and *Astraeus hygrometricus* and *Rhizopogon rubescens*. Nine fungi formed what can be described as non-descript types, i.e. whitish and bruising reddish brown. This type was the most common one observed in the field and the synthesis results indicate that it was formed by a large number of fungi rather than by a dominant symbiont.

5.3.4.3 Growth of mycorrhizal fungi at different water potentials. Each isolate tested on both osmotica was able to grow at higher water potentials on sucrose than on NaCl. For original data, see 1979 report (pages 180-184). This suggests that NaCl is unsatisfactory for determining minimal values for growth but relative tolerance of the different fungi was much the same on the two media. Most species were capable of growth at -1.5 MPa on NaCl and -2.4 MPa on sucrose. *Pisolithus* and *Cenococcum* were the most tolerant to low water potentials as both could grow at -4.8 MPa on sucrose but not at -7.8 MPa. *Laccaria* was the most sensitive of those fungi tested failing to grow on 1.0 and 1.5 MPa on NaCl and sucrose amended media respectively. *Scleroderma* and *Rhizoposom* were both highly sensitive to NaCl but much less so to sucrose.

5.4 LICHENS

5.4.1 Lichen Water Relations

Figure 16a shows the relationship between lichen or duff water content and water potential. The relationships expressed mathematically are: $\psi_t = 75900 \times W^{-1.806}$ and $\psi_p = -2511886 \times W^{-3.29}$

where: ψ_t = Lichen water potential; ψ_p = duff water potential; and w = water content of lichen and duff respectively.

Data from wind tunnel drying experiments are shown graphically in Figure 16b where total resistance to water loss, comprising its two components boundary layer resistance and thallus resistance, is plotted against water content of the lichen carpet. These data show that boundary layer resistance is related to the square root of wind speed. This relationship can be expressed: $r_b = 0.00585\ u^{-0.5}$

where r_b = boundary layer resistance

u = wind speed m sec^{-1}

Thallus resistance is related to water content and can be expressed:

$$r_t = 0.543\ \exp^{-0.0308w}$$

where r_t = thallus resistance

w = water content

Radiation load was found to have little effect on boundary layer resistance. At high water contents, boundary layer resistance is the major factor controlling the rate of water loss, with thallus resistance becoming increasingly important as the lichen carpet dries out. Thus there is a gradual transference of emphasis on the controlling factor as the carpet dries, from external (wind speed) to internal (thallus resistance). During all the intensive runs carried out in 1976, water contents of the lichen carpet in the field rarely exceeded 80%. Thus wind speed would appear to have little influence on evaporation rates in the field.

5.4.2 Ground Layer Water Relations

The diurnal cycle of wetting and drying of the lichen carpet is as follows: typically the lichen carpet began taking up water after sunset, when ambient temperatures were dropping rapidly and relative humidity was increasing. During the night the lichen carpet was able to take up enough water to replace that lost through daytime evaporation. This pattern occurred in all intensive study periods. However when the lichen carpet was saturated by rain, little night-time uptake occurred until water content was reduced to 20-50%. No data on duff diurnal wetting and drying were gathered.

Rainfall interception and retention data were gathered both in the field and laboratory. Laboratory experiments showed that a lichen carpet would intercept and retain an average of 1.77 mm of precipitation before significant infiltration occurred. In comparable experiments, needle duff retained 1.36 mm of rainfall. Full data are presented in

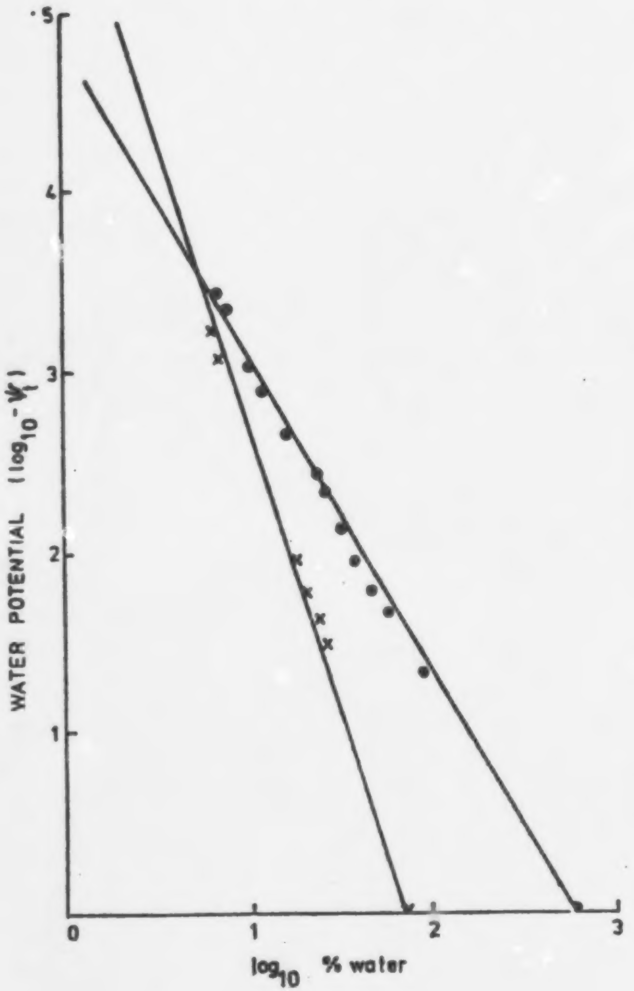

Figure 16a. The relationship between *Cladina mitis* water content and thallus water potential ($-\psi_T$).

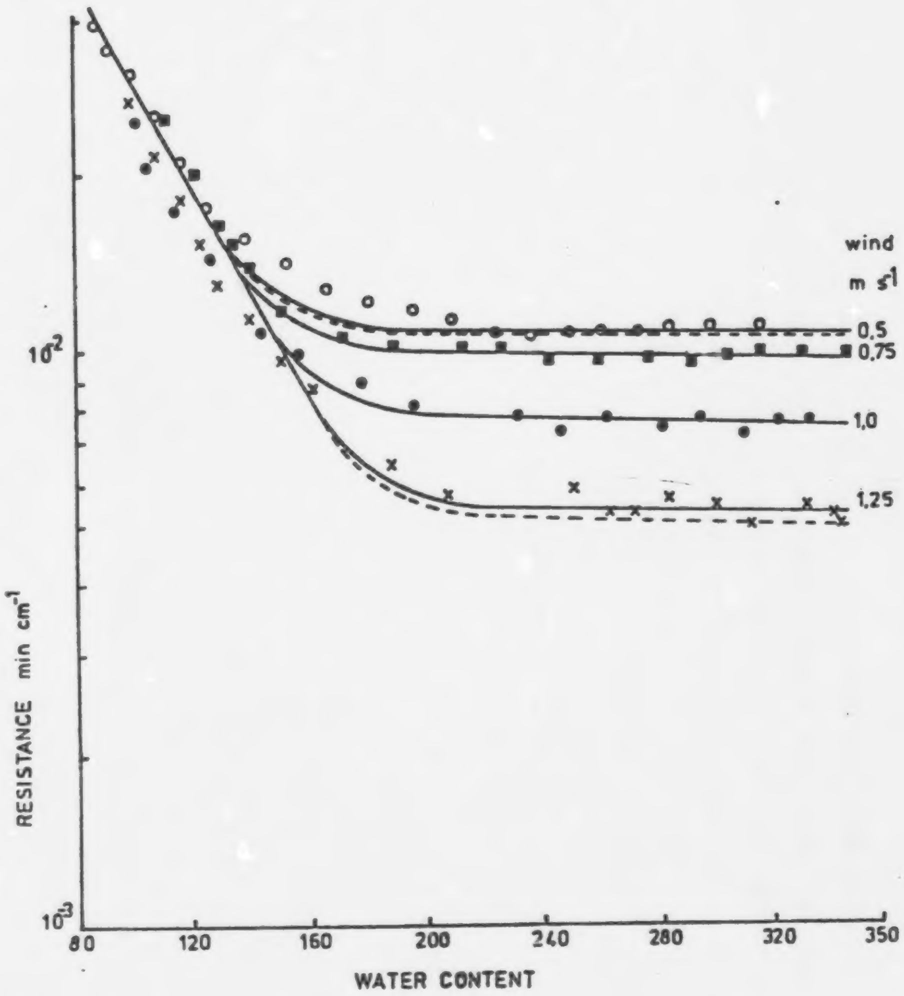

Figure 16b. *Cladina mitis* resistance to water loss at various windspeeds.

Table 10a. Rainfall interception and throughfall data for lichen carpet and needle duff.

Rainfall rate	Rainfall mm	Throughfall mm	Retained mm	% Saturation	No. of runs
Lichen carpet, intact					
20 mm hr^{-1}	0.368	ND	0.368	46.63	1
	0.817	ND	0.817	58.25	1
	1.244	ND	1.244	41.77	2
	3.667	2.119	1.548	58.67	3
	3.732	1.891	1.841	53.04	5
2.2 mm hr^{-1}	1.881	0.037	1.844	69.35	1
Lichen carpet, upper 2 cm					
2.2 mm hr^{-1}	1.129	0.112	1.017	52.89	1
Needle duff					
20 mm hr^{-1}	0.368	ND	0.368	ND	1
	0.733	ND	0.733	ND	1
	3.667	2.265	1.402	ND	3
	3.732	2.301	1.431	ND	3
	4.078	2.886	1.192	ND	1
	4.746	3.827	0.919	ND	1
2.2 mm hr^{-1}	1.881	0.612	1.268	ND	1

Table 10b. Water content (% by weight of soil following precipitation at Richardson Fire Tower, October 1976 (means from six sites).

Sample depth	Bare sand	Lichen carpet	Needle duff
Ground layer	ND	224.1	187.7
Soil surface	14.9	9.8	10.3
Soil 10 cm depth	6.9	6.9	5.5

Table 10. There is some variability in the amounts of rainfall retained by the two types of ground layers, but this is to be expected since the lichen carpet andneedle duff can vary in composition, density, etc. The figure for percent saturation is calculated assuming that the saturated water content of lichen thalli is that obtained in the water potential experiments, i.e., 460%. Percentage saturation figures show that the lichen carpet rarely approaches total saturation, a condition probably impossible to attain under field conditions, but indicate that the carpet has a "field saturation" around 255% (55.5% of total saturation) below which value, throughfall will not occur. Data are incomplete for the needle duff experiments, but indicate that field capacity is similar to total saturation.

Few runs were carried out with prolonged showers, but the data obtained indicate that the ground layer will retain most or nearly all precipitation until "field saturation" is attained. Once this has been reached, throughfall occurs but the ground layer continues to absorb water steadily, approaching total saturation.

Only a small number of gravimetric samples was obtained, since conditions required that they be collected after precipitation and after a long period of dry weather, circumstances that were not too frequent during the 1976 summer at Richardson Fire Tower. Although relatively few samples were taken it is obvious that the ground layer (lichen and/or duff) has acted as a barrier to precipitation penetration (Table 10b). The soil surface being noticeably drier under the ground layer than at sites where there is no plant cover.

5.5 JACK PINE PHYSIOLOGY

5.5.1 Laboratory Studies

Water content, water potential and its components were determined for the trees used in the NA studies. Water content is one of the easiest water parameters to determine and as shown in Figure 17 there is a very good relationship between fresh wt. water content and ψ_L. The linear regression of $\hat{y} = 118.72 + (-1.818X)$ has an $r^2 = 0.71$.
It should be noted that the slope of the line is quite steep making estimates of ψ_L highly dependent upon accurate water content measurements. Figure 18 is a Höfler (1920) diagram relating turgor (ψ_p) and the combined

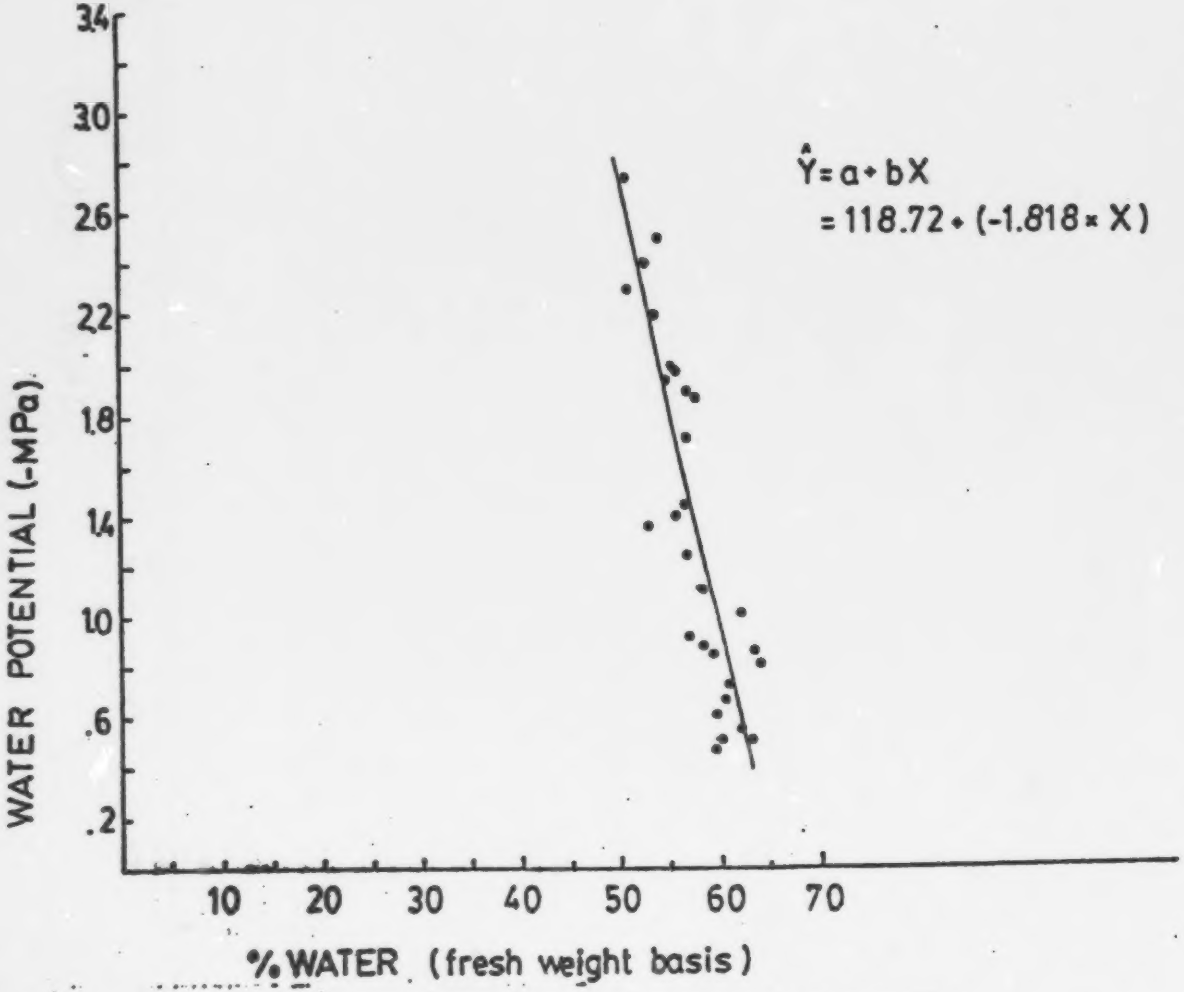

Figure 17. The relationship between Jack pine needle water content and water potential.

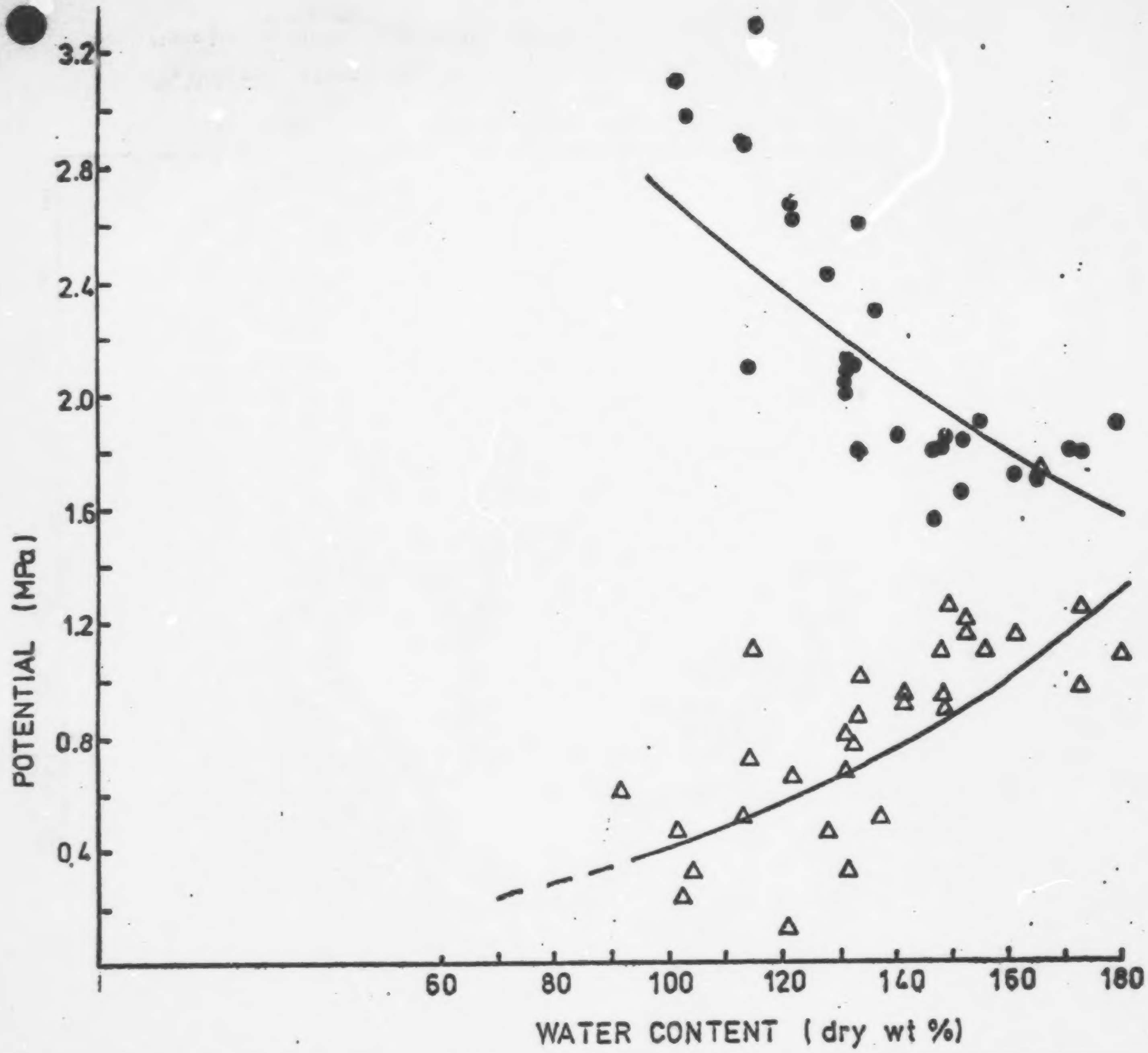

Figure 18. Höfler (1920) diagram of turgor potential (Δ) and combined matric and osmotic potentials (●).

osmotic and matric potentials ($\psi_\pi - \psi_\tau$) to leaf water content on a dry weight basis. The r^2 for an exponential fit of $\psi_\pi + \psi_\tau$ is 0.76. Passive osmotic adjustment due to water loss is apparent changing from a maximum -1.6 MPa to a minimum of -3.4 MPa indicating quite a range with dehydration.

A comparison of ψ_L determined psychrometrically with xylem tension determined with the pressure bomb was carried out in conjunction with the moisture stress study (Figure 19). Although there is considerable difference between the two methods, particularly at low ψ_L, these values are considerably lower than any ψ_L or xylem tensions recorded in the field; and the correlation between xylem tension and ψ_L over the o to -4.5 MPa range is in fact very good. The equation $\hat{y} = 3.82 + 0.82S$ where $\hat{y}$ = psychrometric ψ_L and X = xylem tension has an r^2 of 0.88. However because of the scatter in Figure (the Höfler diagram) the deviation in xylem tension vs ψ_L (Figure 19), and the greater ease of taking Scholander pressure chamber readings, the pressure bomb was chosen as the primary field instrument and except for a few psychrometer readings taken to obtain seasonal $\psi_\pi + \psi_\tau$ measurements it was used exclusively.

The results of the drying-survival study are given in Figure 20. The dashed line is the approximate division between minimum damage and severe damage with a high probability of death. It is apparent that xylem tensions of 3.5 MPa to 4.0 MPa will result in severe damage even when the plants are given the best of care after the stress. The results suggest that as drying time increases, the dividing line occurs at higher water potentials. Interestingly enough when the plants were dried to 3.5 MPa ψ_{leaf} during the NA study, one of the plants failed to recover. Thus, there is good agreement between the two studies. Stress symptoms were assessed after 3 weeks in a humid greenhouse where the plants were well watered. They were given a final evaluation at 15 weeks to determined whether or not some of the severely injured plants had recovered or died. The following descriptions were used in Figure 20.

Minimal damage (●); perfectly healthy trees to those with a few necrotic spots or bands, often on the 1st year main axis and newer needles.

Severe damage (■); extensive necrosis, spots or bands, and/or chlorosis at 3 weeks. Sometimes only the older needles surviving. The younger needles often severely necrotic. After 15 weeks 32% of these plants were dead (⊡).

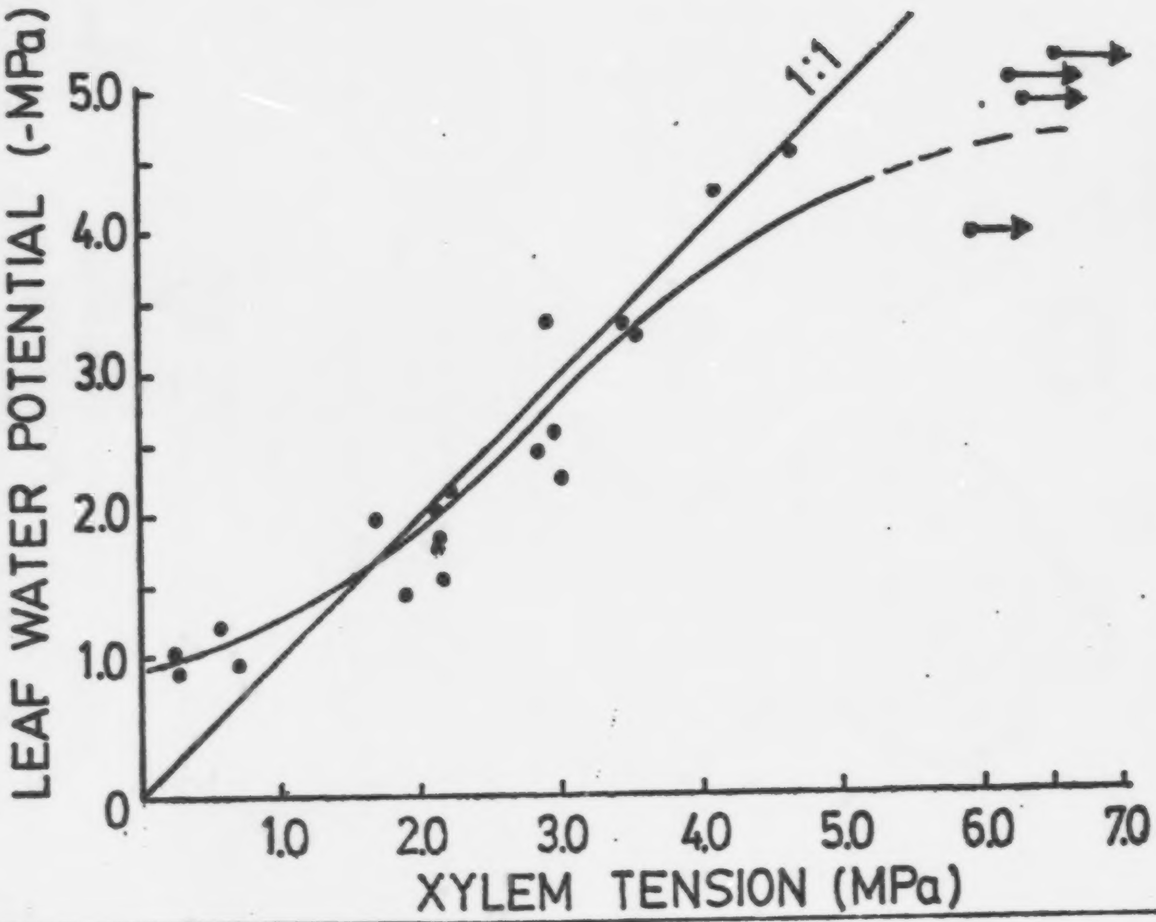

Figure 19. The relationship between Jack pine xylem tension and psychometrically determined leaf water potential. Arrows indicate xylem tensions off scale.

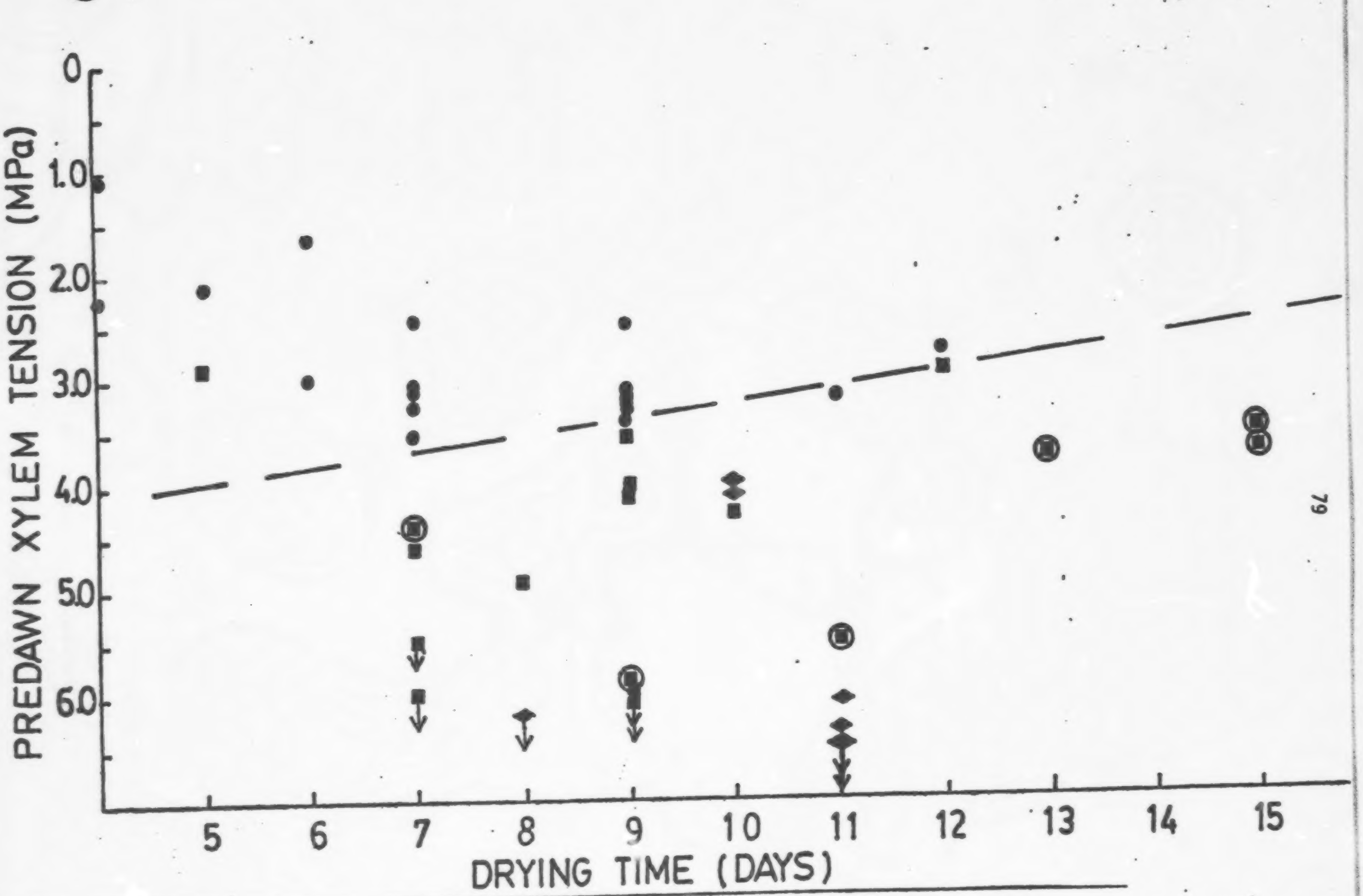

Figure 20. Survival of drought stressed young Jack pine at various xylem tensions as a function of drying time:
● = no damage; ■ = damage but survival at 3 weeks recovery after watering; ⊡ = damaged but survival at

Dead (◆); dead at three weeks.

The effects of drying upon the NA of 4 trees are shown in Figure 21. The first cycle was stopped prior to zero NA because of equipment problems although the trees were dried to somewhat less than -.8 MPa ψ_{leaf} . Even so, NA did not recover to the prestress value of 8 mg CO_2 dm^{-2} h^{-1}. NA reached zero in 6 days during the second cycle and ψ_{leaf} was -2.2 MPa at that point. The plants were dried further to an average xylem tension of 3.5 MPa before being watered. This is very near the lethal limit for Jack pine (see Figure 20) and in fact one of the plants did not recover. Its leaf water potential only recovered to -1.0 MPa whereas the other 3 plants recovered to -0.5 MPa, the prestress value. Only the results of the trees that recovered are shown in Figure 21, cycle 3. Day zero, cycle 3, was actually started 10 days after the plants were rewatered thus cycle #3 represents recovery after extreme stress, but not immediately.

5.5.2 Field Studies

Needle water content, by age class, is shown in Figure 22. In 1976, water contents of all age classes decreased during the early summer months to a low in late June, but increased again to approach the spring high by late August. In 1977 the pattern was similar to 1976 at least until the project termination. Water contents of needles decreased with increasing age. The relationship of xylem tension to water content shifted through the season and linear regression of the relationship were very poor ($r^2 < 0.14$). These results suggest that it would be very difficult to estimate xylem tension from water content. (It should be noted that relative water content, RWC, was not suitable for the purposes of modelling and determining water budgets. Accordingly actual water contents were used.)

Xylem tensions and soil moisture tension at 20 cm, measured at the middle site, are given in Figure 23. It is noteworthy that soil moisture tensions were always low. The maximum being only ca. 0.04 MPa as measured with tensiometers. Neutron probe moisture contents converted to tension via Figure 8 agreed with these results indicating that soils were generally moist and not too far from "field capacity" most of the time thus the xylem tensions are for well watered trees. It is interesting to note that the changes in needle water content (Figure 22) occurred in

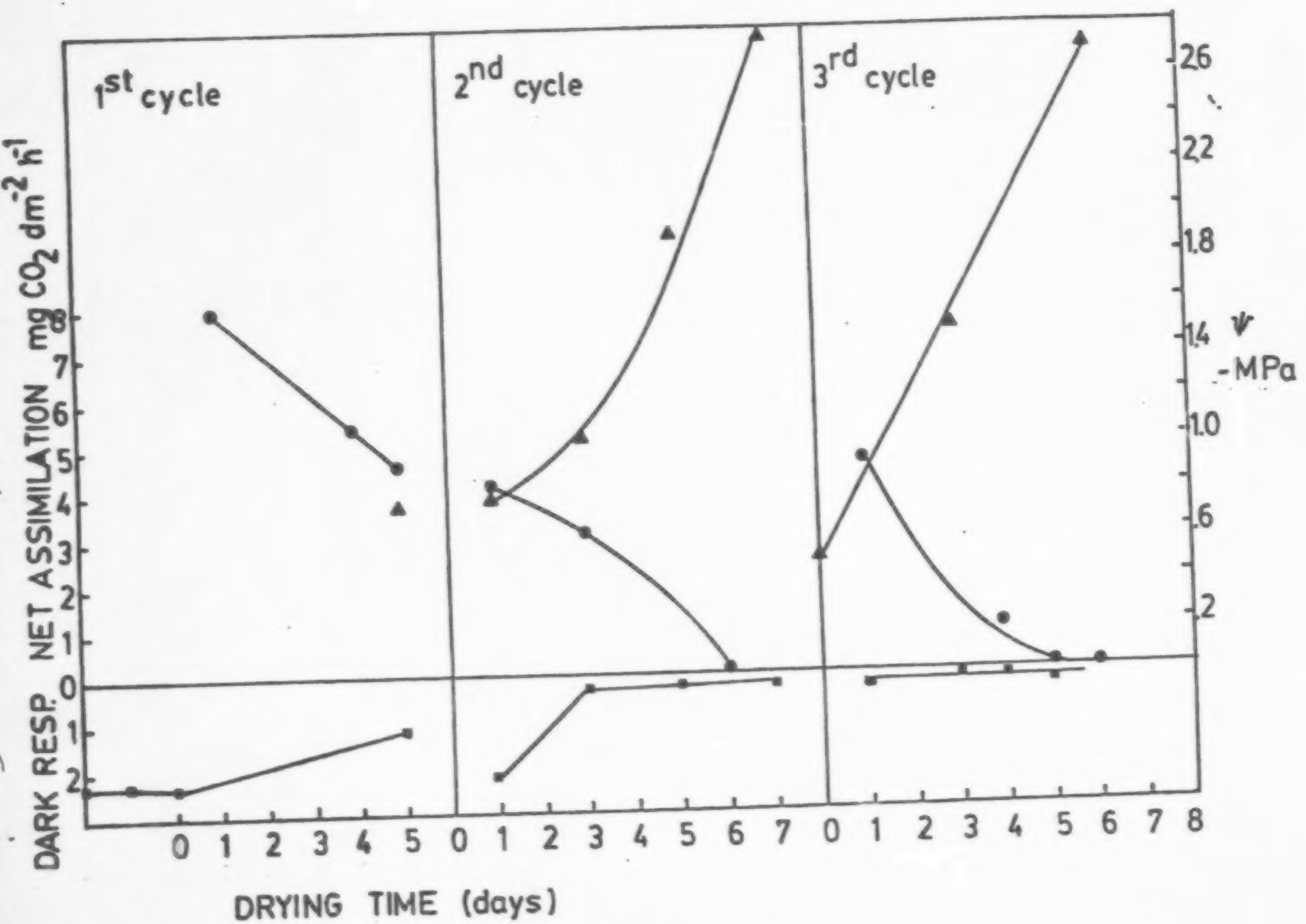

Figure 21. Net CO_2 assimilation (●), dark respiration (■), and needle water potential (▲) of drought stressed Jack pine.

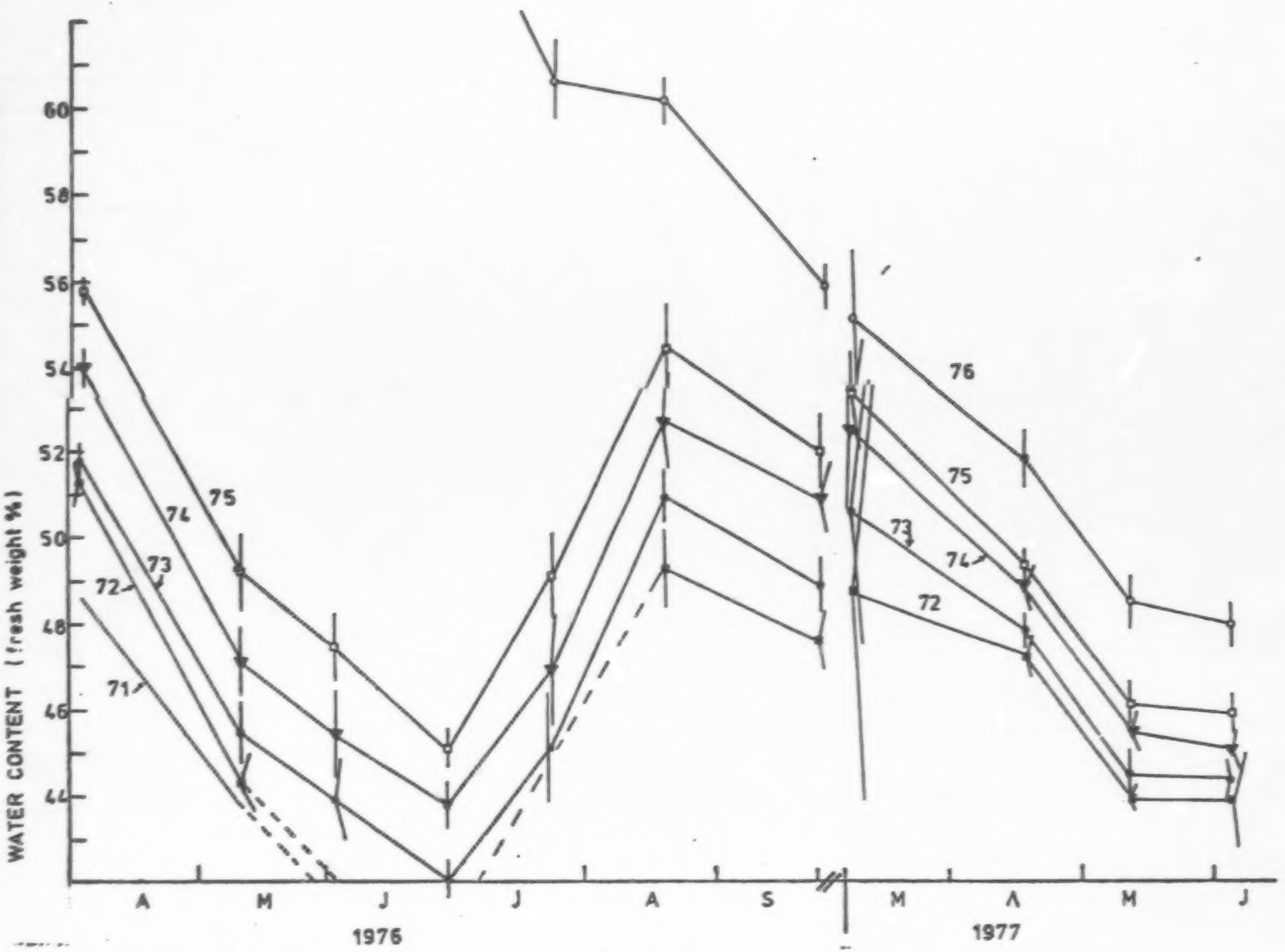

Figure 22. Mean Jack pine needle water content (fr. wt.) by age class during 1976, 1977. Vertical bars are 95% confidence intervals.

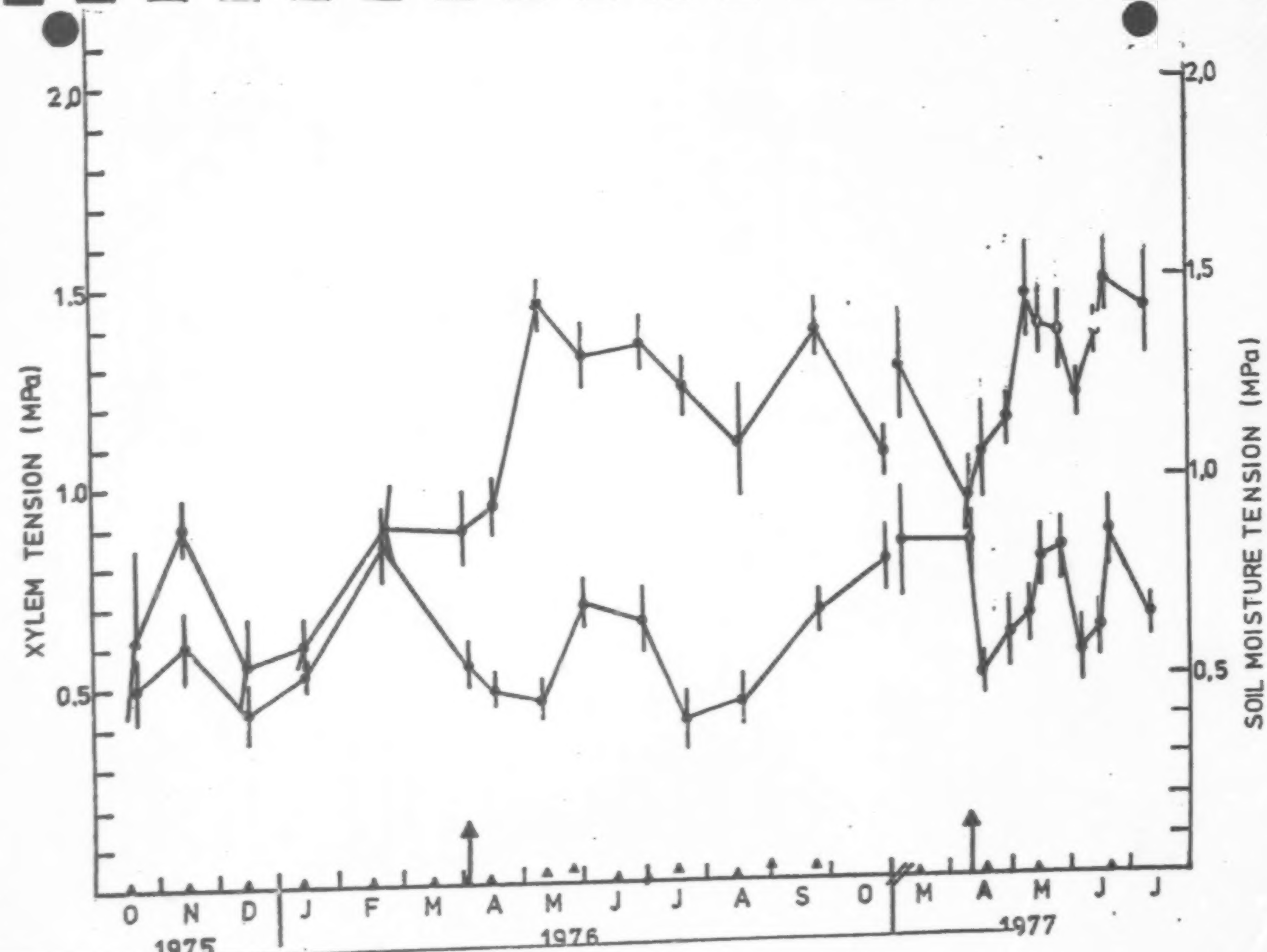

Figure 23. The seasonal course of minimum (dawn) and maximum (midday)
xylem tension (•) of Jack pine at the midslope study site
Vertical bars are 95%

well watered trees. There were no statistical differences between dawn and midday xylem tensions of trees at the top or bottom of the hill compared with those at the middle site (see previous reports).

Water potentials and its components are given in Table 11. Generally xylem pressure potentials (-xylem tension) are higher than ψ_L. Combined osmotic and matric potentials are remarkably stable throughout the year. The relationship between water content and ψ_L varied depending upon needle age. The linear relationship between ψ_L and water content for 1975-76 needles was $\hat{y} = 79.0 - 1.37S$, ($r^2 = .8$), where: $\hat{y} = \psi_L$ and X = water conten For the 1971-74 needles the relationship was $\hat{y} = 94.5 - 1.8X$, ($r^2 = .8$).

The effect of radiation upon R_L is shown in Figure 24. The data was taken on June 29-30, July 21-23, and August 16-20 during which the maximum xylem tensions were respectively 1.5 MPa, 1.4 MPa and 1.6 MPa. As shown in Figure 23 soil moisture tensions were very close to field capacity. A boundary line analysis (Webb 1972; Jarvis 1976, and Hinckley 1978), shown in Figure 24, indicates the R_L mean minimum to be on the order of 6 scm^{-1} with nearly full opening occurring at 200 $\mu Em^{-2}\ s^{-1}$ PhAR. The equation for the boundary line analysis is:

$$Y = ax^b$$

where: $Y = R_L$; $a = 27158$; $b = -0.53$ and $r^2 = 0.83$

Leaf resistances rather than conductances are reported throughout the paper because of the modelling that required us to look at water movement from soil to the atmosphere as a series of fluxes and resistances. To quote Hall et al. (1976) "Resistances are, however, more convenient than conductances when the effects of a catenary series components are partitioned".

The results of R_L vs xylem tension when VPD was low and PhAR $\geq 200\ \mu Em^{-2}s^{-1}$ are shown in Figure 25. They suggest very little effect of xylem tension until 1.2 MPa or higher and certainly no great effect until 1.4 MPa. This was the basis for the modelling xylem tension vs R_L. The very high R_L values at low xylem tension are due to VPD induced closure. It was apparent in 1976 that vapor pressure deficits could cause stomatal closure accordingly in 1977 more measurements were taken by the diffusion porometer technique. The results for May 11 and June 1, 3, 4 are shown in Figure 26. The maximum xylem tensions for these periods were 1.10 MPa or

Table 11. Seasonal leaf water potentials (ψ_L), osmotic plus matric potentials ($\psi_\pi + \psi_\tau$) turgor potentials, and xylem tension of Jack pine. Values are means ±95% confidence limits in Mega Pascals (MPa).

Date	Xylem tension	ψ_L	$\psi_\pi + \tau$	ψ_p	Notes
13/XI/75	.63[a]	-1.05 ± .33	-2.29 ± .30	1.24 ± .41	75 needles only, 0630 hr
15/XII/75	.48 ± .14	-1.14 ± .30	-2.38 ± .42	1.23 ± .42	75 needles only, 0830 hr
12/I/76	.54 ± .06	-.71 ± .25	-2.35 ± .25	1.61 ± .29	75 needles only, 1005 hr
20/II/76	.95 ± .06	-.84 ± .16	-2.31 ± .30	1.48 ± .30	75 needles only, 1430 hr
4/IV/76	.57 ± .04	-.79 ± .21	-2.33 ± .35	1.54 ± .33	75 needles only, 0645 hr
16/IV/76	.50 ± .05	-1.14 ± .60	---	---	75 needles only, 0510 hr small sample
11/V/76	.60[a]	-1.14 ± .20	-2.30 ± .20	1.19 ± .22	72-75 needles, 0630 hr
3/VI/76	1.0[a]	-1.41 ± .25	-2.42 ± .31	1.01 ± .28	72-75 needles, 1200 hr
27/IX/76	1.6[a]	-2.25 ± .22	-2.90 ± .16	.76 ± .20	72-76 needles, 1200 hr
27/IX/76	1.6[a]	-1.91 ± .17	-2.94 ± .14	1.03 ± .21	75-76 needles,
27/IX/76	1.6[a]	-2.49 ± .27	-2.87 ± .33	.51 ± .22	72-74 needles
9/III/77	.72	-.73 ± .08	-1.95 ± .09	1.22 ± .09	72-76[b] needles, 1000 hr
19/IV/77	.47	-.80 ± .11	-2.31 ± .09	1.51 ± .14	73-76 needles, 0500 hr
19/IV/77	1.15	-.96 ± .16	-2.41 ± .12	1.45 ± .16	73-76 needles, 1050 hr
12/V/77	1.31 ± .20	-1.72 ± .14	-3.0 ± .14	1.29 ± .15	73-76 needles 1415 hr
6/VI/77	---	-1.41 ± .15	-2.41 ± .11	1.00 ± .11	71-77 needles, 1315 hr

[a] All psychrometric samples taken from one branch, therefore only one Scholander reading.

[b] When needles of different age classes were mixed in the sample, there were no large differences between them.

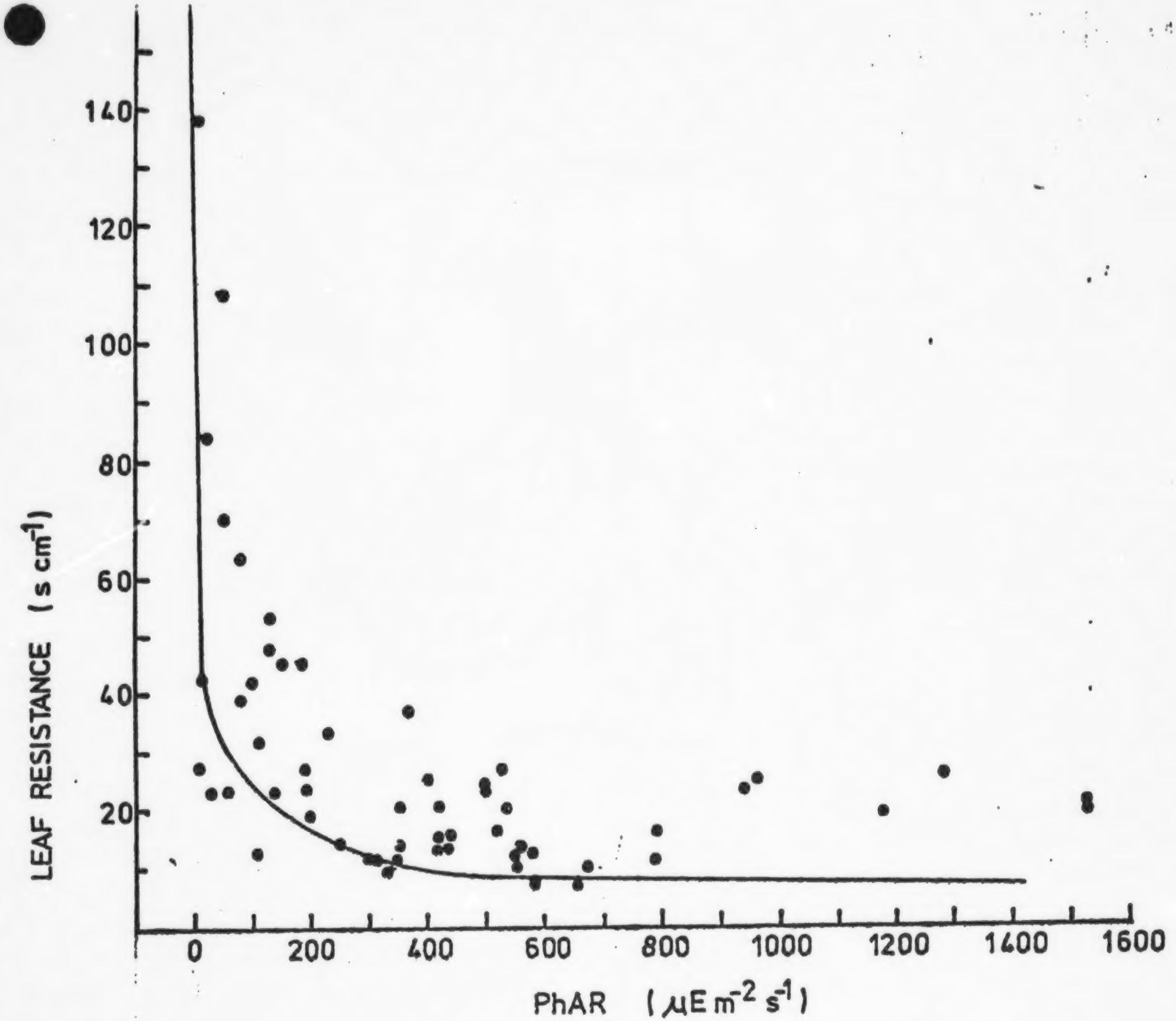

Figure 24. The relationship between Jack pine leaf resistance (needled clump-all age classes) and photosynthetically active radiation (PhAR = 400-700 nm).

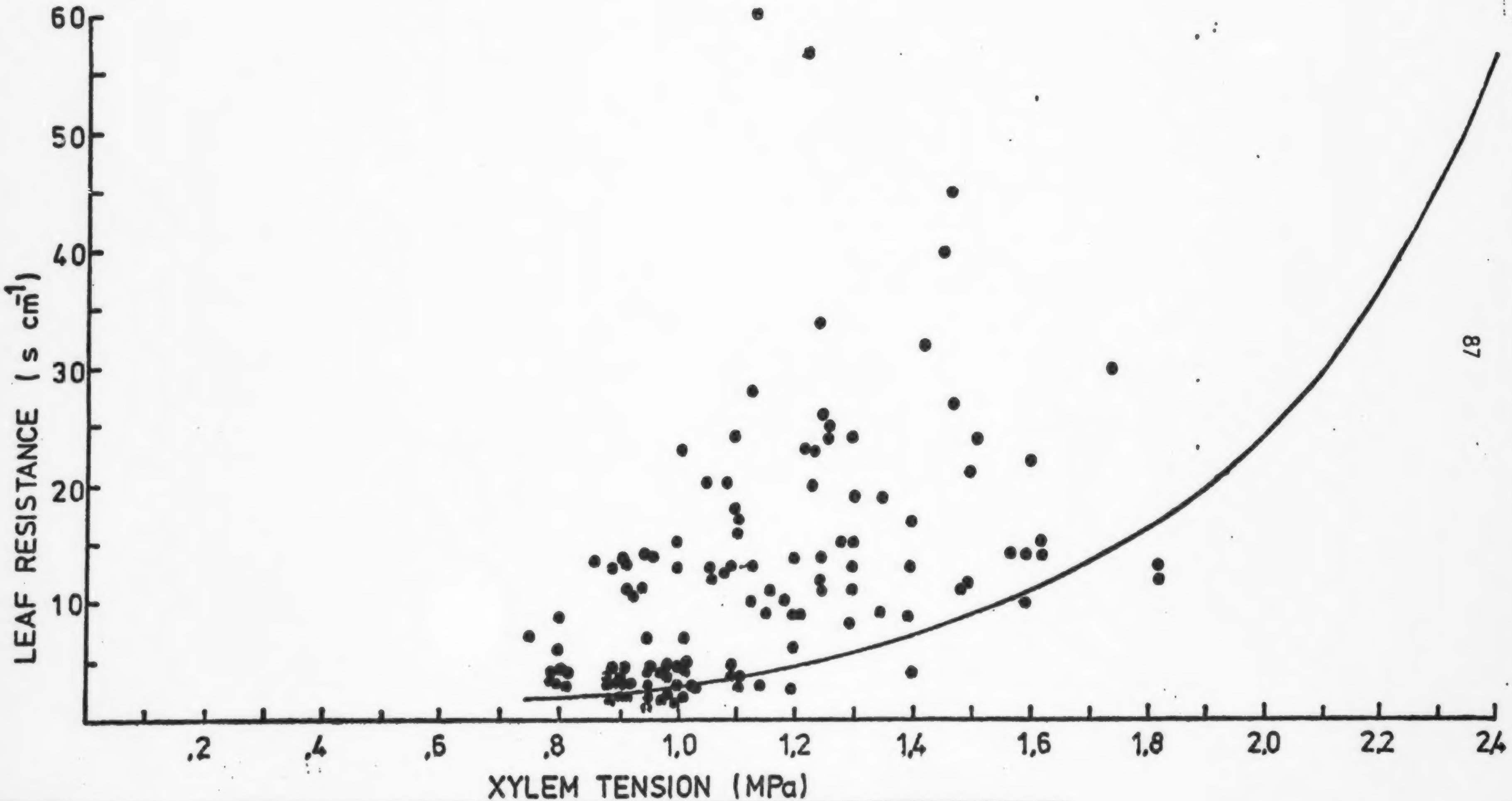

Figure 25. The relationship between Jack pine leaf resistance and xylem tension. Solid line is a boundary line analysis where $\hat{y} = ae^{bx}$ and $a = 0.372$, $b = 2.097$, X = xylem tension, $\hat{y} = R_l$.

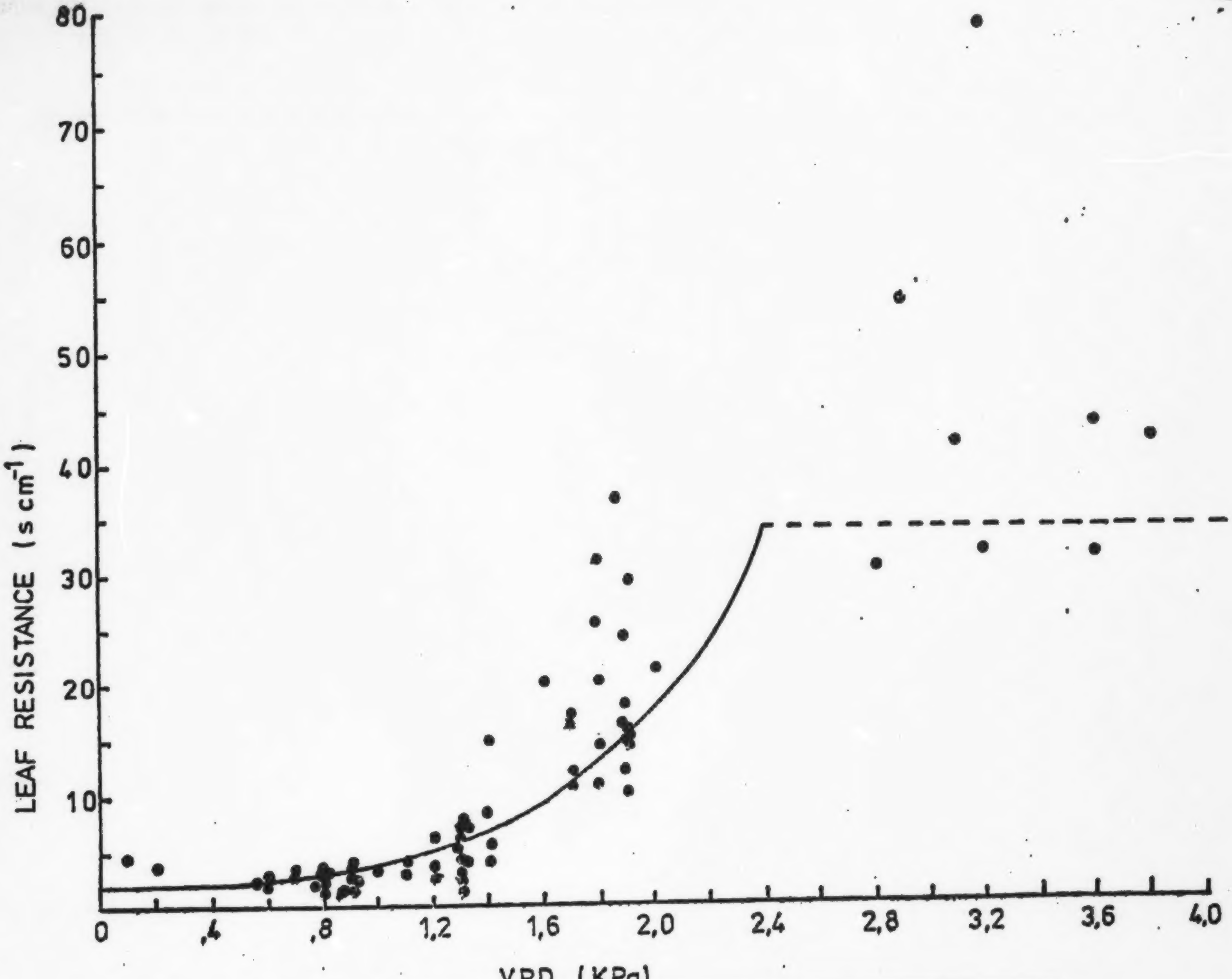

Figure 26. The relationship between Jack pine leaf resistance and vapour pressure deficit (VPD). Solid line is a boundary line analysis and dashed line a visual fit of maximum D.

less, values that on days with low VPDs allowed minimum resistances of 5 scm^{-1} or less thus indicating that xylem tension was not the cause of stomatal closure.

We were fortunate enough to be on site during the period of maximum snow melt both years, when air temperatures were well above zero (25°C) and the snow literally melted in a few days. This occurred on April 3-4, 1976 and April 8, 9 and 10, 1977. A period of intensive measurements on April 3-4, 1976 showed that leaf resistances were well above 100 scm^{-1} and xylem tensions were on the order of 0.6 to 0.8 MPa throughout the study period suggesting that maximum stomatal functioning does not begin rapidly with warm temperatures. Because of these results an attempt was made to obtain fall and early spring R_L values to see if in fact winter stomatal closure is a [illegible]. The fall values were taken on October 28, 1976. Even though VPD was only 0.6 KPa, soil and air temperatures were above freezing (8.6 and 3.4°C respectively) and xylem tensions were not particularly high (max 1.23 MPa), the R_L values at 1200 h and 1530 h were respectively 67.6 scm^{-1} and 84.8 scm^{-1} suggesting stomatal closure with the onset of dormancy perhaps due to the short days. Diurnal measurements of xylem tension and R_L were begun on March 8, 1977. This was prior to snow melt; however, air temperatures were above freezing (11°C). Mean leaf resistances were well above 100 scm^{-1} (as high as 680 scm^{-1}, i.e. within the leak rate of the porometer) throughout the day even though xylem tensions were not particularly high (1.5 MPa or less throughout the day). The stomata were obviously closed tightly. Intensive studies were carried out on April 8, 9, 10, 1977 during which time air temperatures rose to 25°C and leaf temperatures to 27°C. Xylem tensions were on the order of 0.9 MPa yet R_L values were 150 scm^{-1} or more, thus proving closed stomata. By April 15-16, 1977, there was partial stomatal opening (R_L = 18 scm^{-1}). These studies suggest a progressive decrease in minimum leaf resistance associated with warming of the soil. Figure 27 shows the relationship between minimum R_L and soil temperature. Soil moisture and xylem tensions were not sufficiently high to cause stomatal closure (during the summer periods) and with the exception of April 8, VPDs ranged from 0.7 to 1.0 KPa and would not cause closure (Figure 26). Even th 2.3 KPa VPD on April 8 would not cause such complete closure.

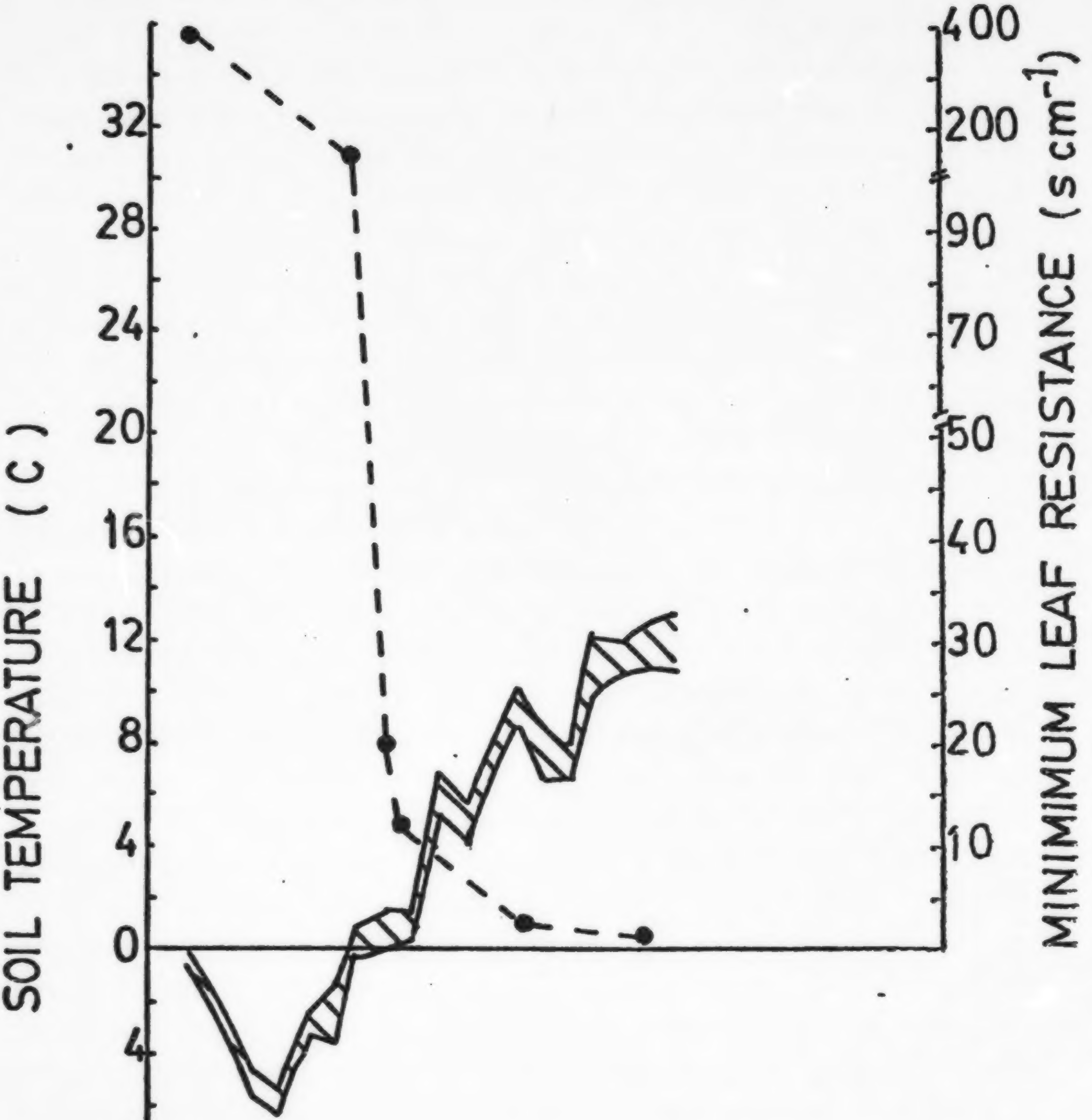

Figure 27. The relationship between root zone soil temperature (max and min) and minimum leaf resistance as the season progresses.

5.6 MODELS

5.6.1 Radiation Model

The reader is referred to this 1979 AOSERP report for a more detailed treatment of the model output. Several treatments of radiation attenuation are presented. Figure 28 shows the comparison of measured radiation and model output when the canopy is treated as cone-topped, flat-topped having the same height, density and spacing as the pointed trees. Comparisons of predicted and measured values of radiation transmission were made for the three kinds of canopy (i.e. cone top, flat top or random). These were further divided into visible and near infra red. The cone topped model accounts reasonably well for afternoon measurements while the morning measurements seem to fit between the flat-topped and random models. Figure 29 shows the results for flat-topped trees. It is felt that this model is adequate for the energy and water balance model.

5.6.2 Energy and Water Balance Model

The model was tested by comparing it with measurements from May 7 to August 31, 1976. Figure 30 shows predicted needle water potentials and measured xylem tensions for several intensive study periods. Figure 30 shows seasonal maximum and minimum needle water potentials predicted by the model. Figure 31 shows the cumulative loss of water by transpiration compared with cumulative loss from the soil. The results are, in general fairly good.

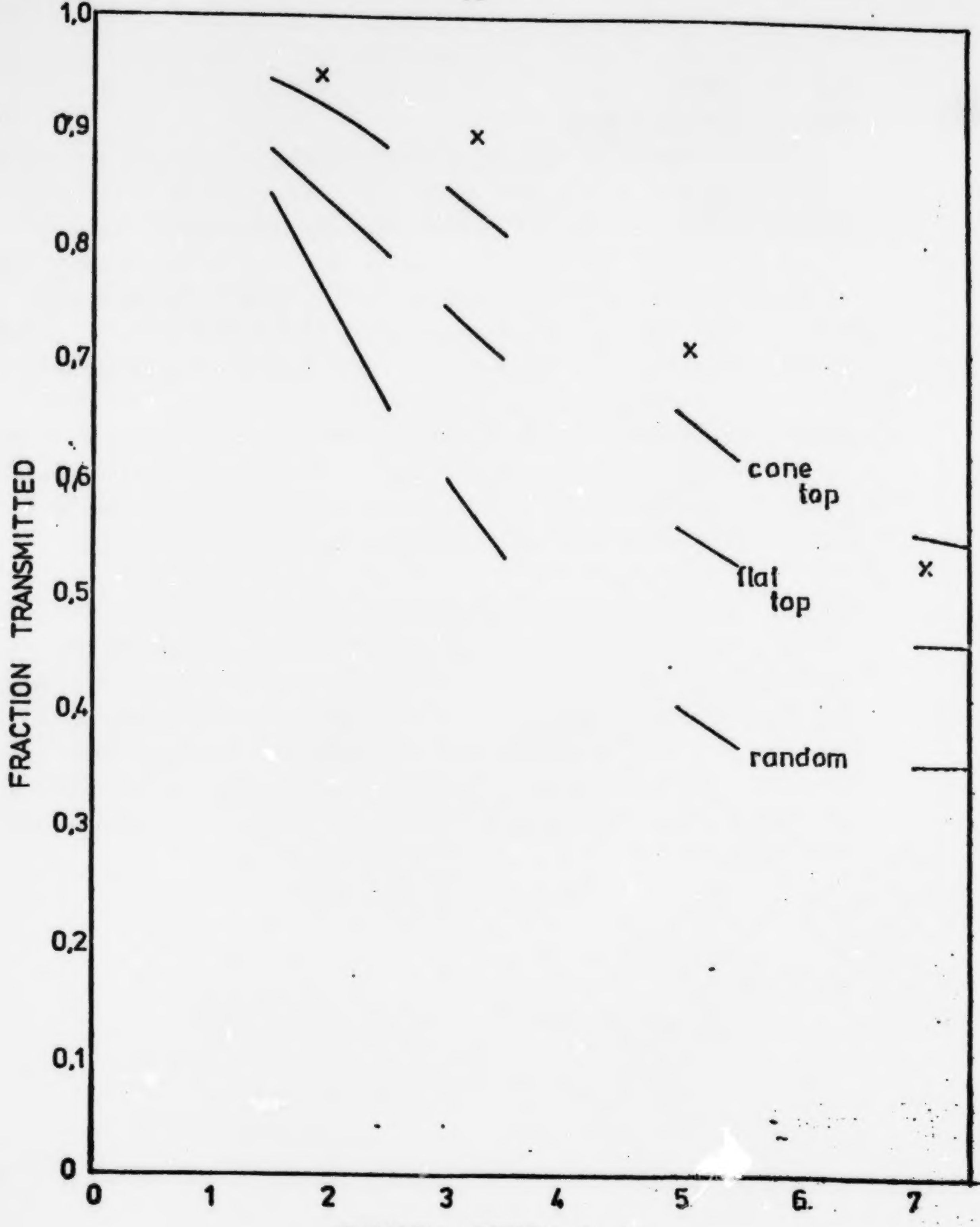

Figure 28. Comparisons of measured radiation transmitted with three types of model canopies.

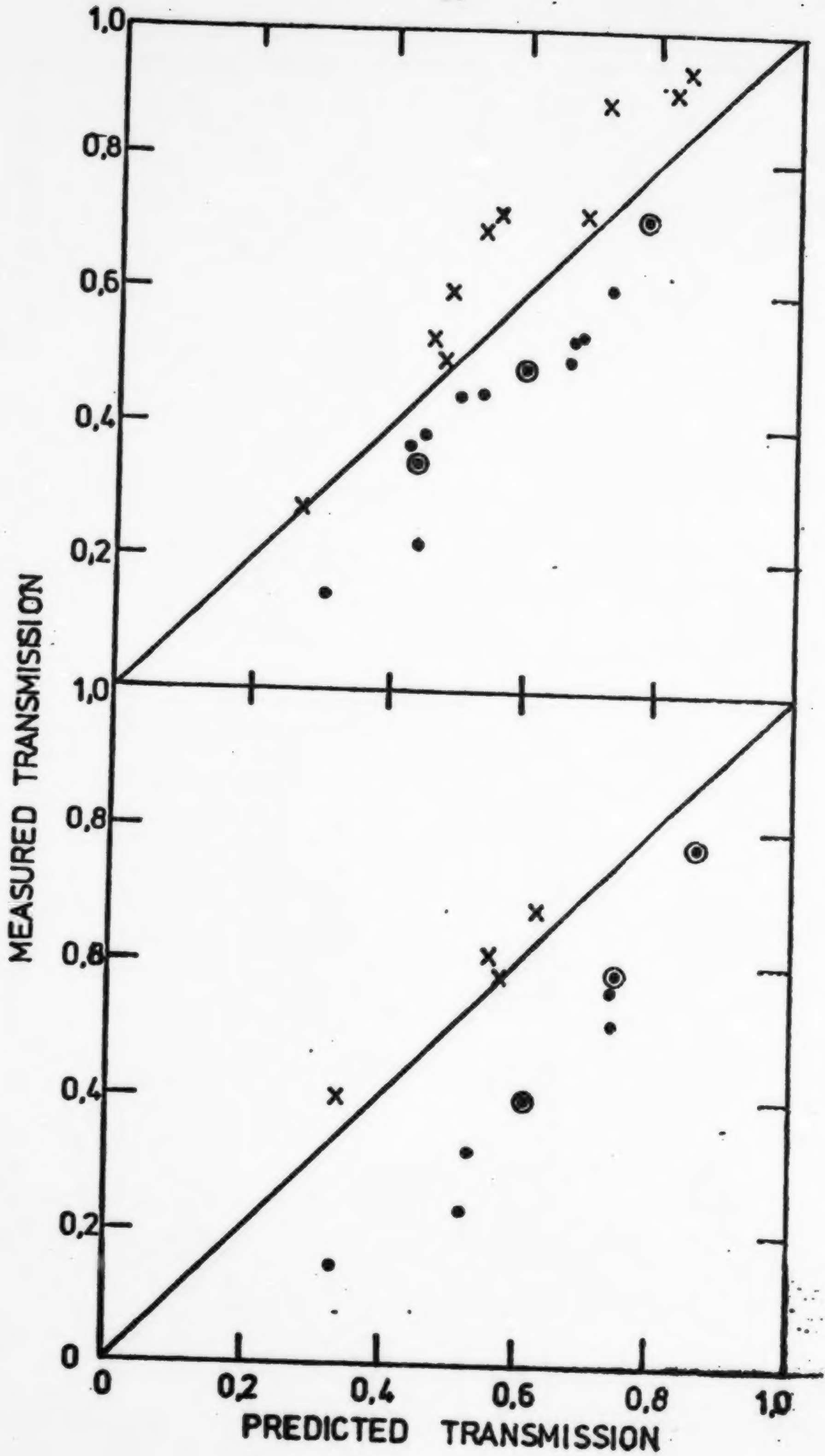

Figure 29. Measured vs predicted radiation transmission through the Jack pine canopy. Upper is visible; lower near infrared.afternoon (x); morning (•); sun below hill (◉).

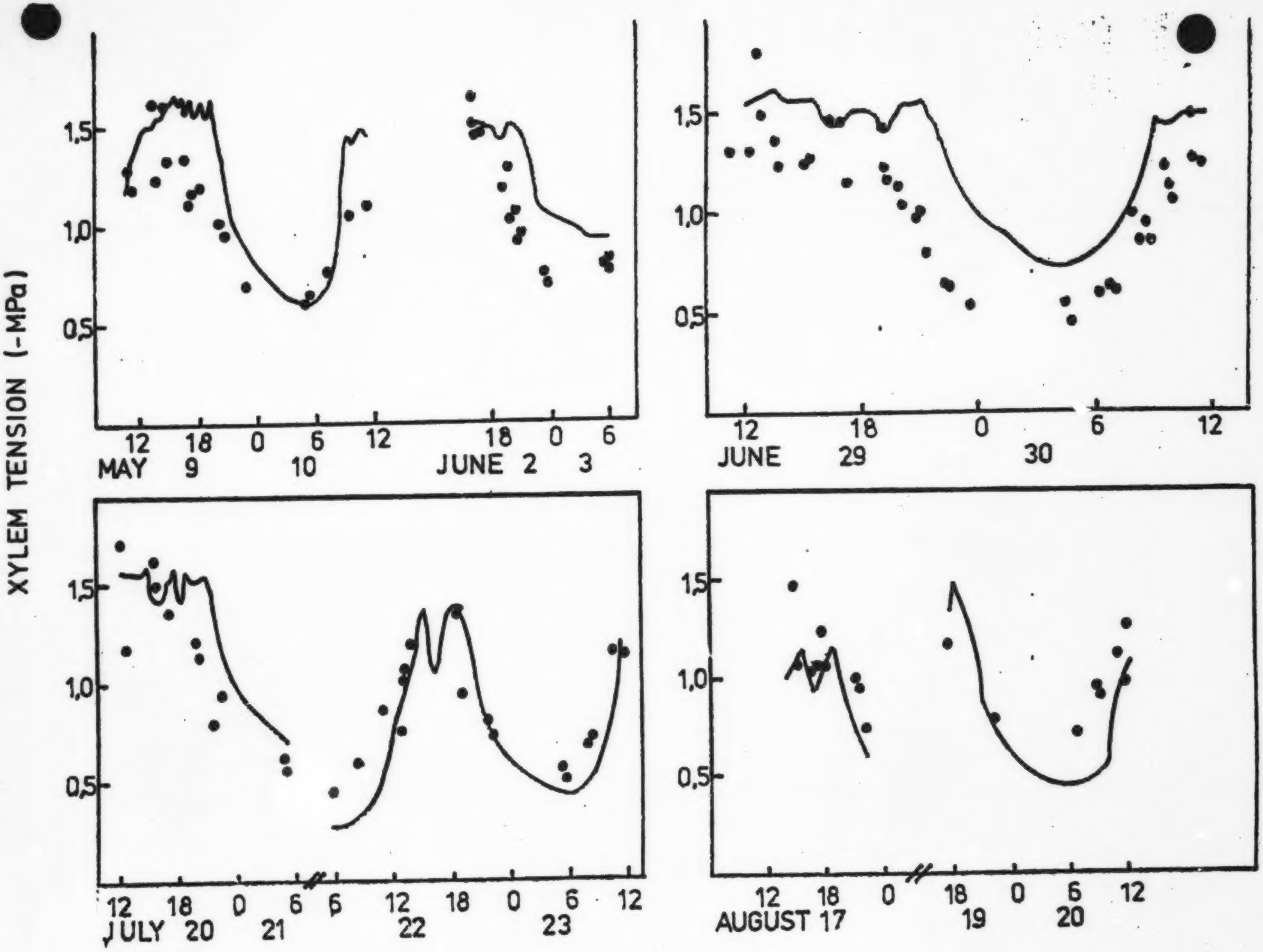

Figure 30. Diurnal trends of measured and modelled branch xylem tensions at several dates during 1976. Modelled = solid line, measured = dots.

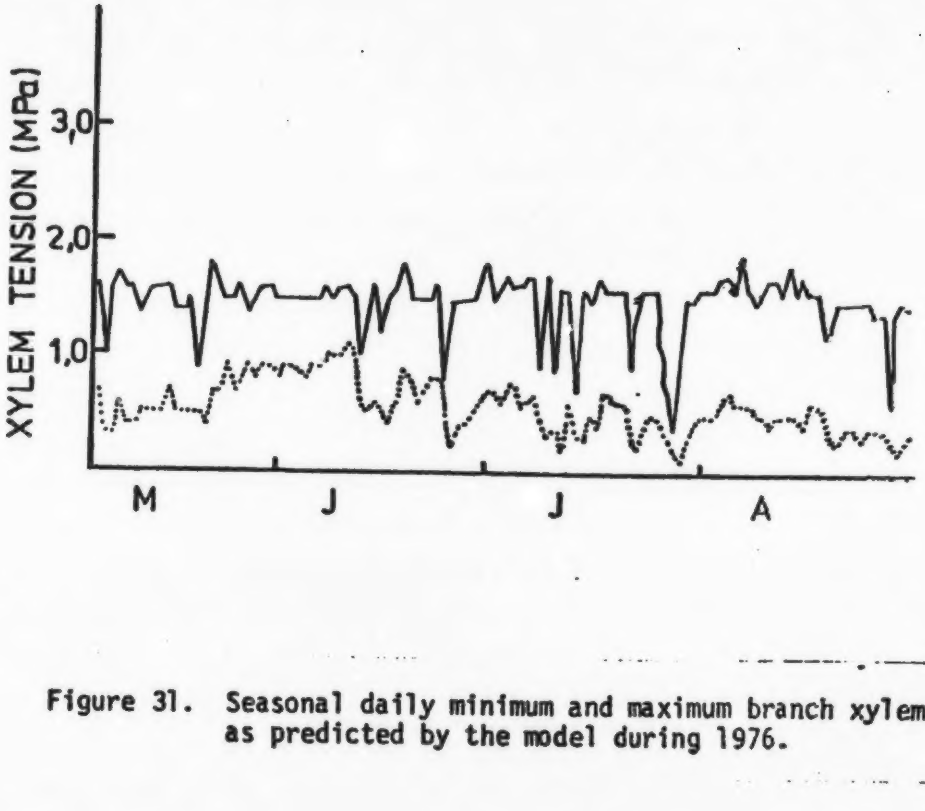

Figure 31. Seasonal daily minimum and maximum branch xylem tensions as predicted by the model during 1976.

6.0 DISCUSSION

The long term weather records show that the Richardson site is generally warmer and drier than the Fort McMurray airport (Figure 32, Table 12, Table 5, Figure 15). The southwest slope was in fact drier than the fire tower station at the top of the hill (Table 12). The weather was similar for the two study seasons except for August, 1977 (Table 5). The high frequency of cyclonic storms and associated increased cloudiness resulted in less radiation, lower temperature and higher precipitation during August. The high storm frequency, especially in 1977 (Figure 15) resulted in low soil moisture tensions (Figures 8, 10, 23). Because of turbulence due to the forest canopy, the exposed nature of the slope, and low tree density, it was difficult to locate sources and sinks for temperature, water vapor and wind. Gradients tended to be small and ill-defined. The canopy is effective in intercepting precipitation from light rains (1-3 mm); this along with lichen interception (Table 10a) and the extreme porosity of the soil (Table 4) contribute to the xeric nature of the site as well as its resistance to erosion.

Following precipitation, the sand at the Richardson site drains rapidly to 10% moisture (by volume) in the Ae horizon and 6% at ca. 30 cm. This corresponds to tensions .01 MPa (Figures 8 and 10). The tension at "field capacity" is approximately 0.06 MPa. There is approximately 95 mm of available water in the Ae and 58 mm in the deeper sand of the root zone. Thus the soil has little available water between "field capacity" (0.06 MPa) and "permanent wilting (1.5 MPa) as shown in Figure 8. Plants growing on such sand must be conservative of water use and/or drought tolerant. In spite of the low water holding capacity, periods of high soil moisture stress were not observed (Figures 8, 10, 23). This was due to the frequent rains (Figure 15), the tendency of Jack pine stomata to close during periods of high VPD (Figure 26), and the evaporation retarding effect of the lichen layer (Figure 16b). Approximately 48% of the precipitation is lost to plants through drainage (Figures 10 and 11), thus increased sorptivity through soil amendments (e.g. Takyi et al. 1977) could increase the amount of available water retained in the root zone. Another factor in deep drainage is that the ground water basin have the capacity to absorb such a high percent of the precipitation. If, as in the dike system, the

Table 12. Total monthly precipitation data for Richardson, Richardson Lookout and Ft. McMurray Airport (mm)

Station	MAY	JUNE	JULY	AUG.	TOTAL
Ft. McMurray A. (1941-1970)	33.0	61.5	73.7	64.0	232.2
Richardson Lookout (1941-1970)	24.9	56.6	57.4	73.4	212.3
Richardson (our site) (1976)	22.3	71.9	67.7	33.3	195.2
(1977)	57.7	43.2	85.4	46.0	232.3

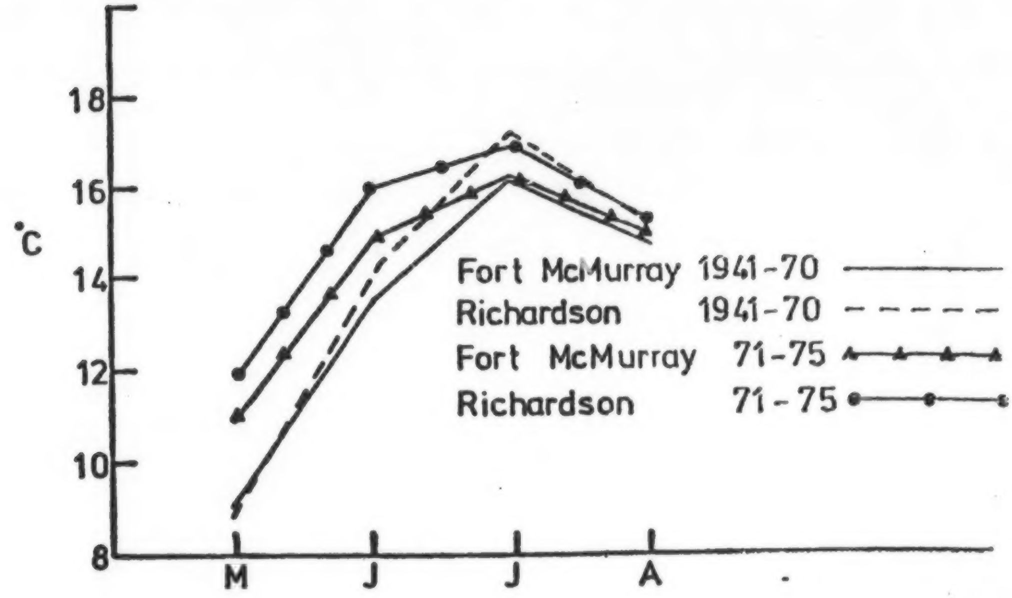

Figure 32. Mean monthly temperatures for the Fort McMurray airport and the Richardson Firetower study site.

sand rests on an impermeable layer, toe slumping such as shown in Rowel (1977) may result. Increased sorptivity of the upper layers may help to prevent this sort of erosion. The sands at the Richardson site and the tailings dikes, even though not identical, are highly erosive (Takyi 1977, Rowel 1977, 1978, 1979). It is essential that they be protected from raindrop splash action and that infiltration at least equal non-intercepted precipitation. The grasses on the tailings dikes and the pine-lichen cover at Richardson both protect the soil from direct raindrop detachment leaving infiltration as a major concern. The very high saturated conductivity of the Richardson sand (Table 4, Figure 7) ensures that during spring thaw there will be little erosion. The maximum storm recorded at the Richardson site was 28.4 mm h^{-1}, and the 25 year maximum for Fort McMurray is 28 mm h^{-1} (Brace 1959). This intensity is not particularly great thus accounting for the presence of stable sand slopes such as the Richardson hill and offering some hope for sand dikes. However the hydraulic conductivity of the Richardson sand is considerably greater than that of tailings sand. Saturated conductivities (Table 4, Figure 7) of 26.6 to 57.6 cm h^{-1} compared with 5.7 to 8.7 cm h^{-1} for unamended tailings, and 18.7 to 32.8 cm h^{-1} for peat amended tailings (Rowel 1977) illustrate the greater porosity of the Richardson sand and probably a major difference between the sites. A comparison of conductivity of unsaturated tailings and Richardson sand is given in Figure 33. Two salient features of Figure 33 are: 1) the greater saturated hydraulic conductivity of the Richardson sand; and 2) the very rapid decline in conductivity with drying. Both sands have very low conductivities at 0.1 MPa; well below the maximum storm intensity. Taylor and Ashcroft (1972) state that two factors are involved with infiltration: 1) storage; and 2) transmission. They discuss the equation derived by Philip (1957);

$$i = Sp't^{\frac{1}{2}} + Ap't$$

where: i = the quantity of water infiltrating a cross sectional area of soil. Obviously $i \geq$ non-intercepted precipitation if overland flow is to be prevented.

Sp' = The sorptivity of the soil

t = time

Ap' = a parameter that depends on the soils ability to transmit water.

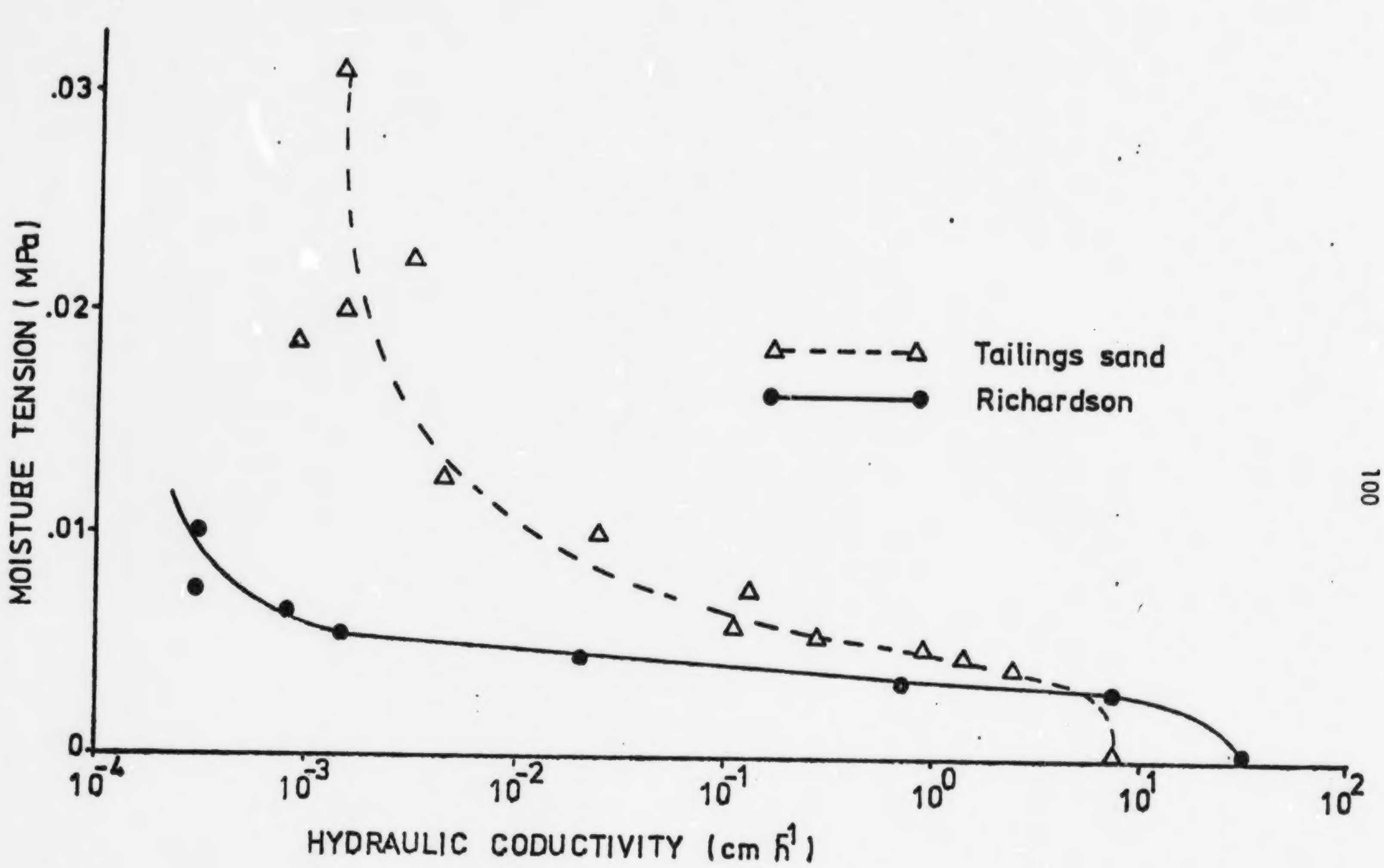

Figure 33. The relationship between hydraulic conductivity and soil moisture tension for Richardson (horizon sand and GCOS tailings sand).

Sorptivity (Sp') decreases as the water content of the soil increases thus explaining the decrease in infiltration with time starting with an initially dry soil (Taylor and Ashcroft 1972). As Sp' decreases $i \approx Ap't$ and eventually $i/t = Ap' = K$ the hydraulic conductivity of the soil. They further show that Ap' and Sp' are dependent upon initial soil water content. Ap' increases with initial H_2O content and Sp' decreases (at a much greater rate). Regarding the Richardson and/or tailings sands it is important to realize that Sp' may be very nearly negligible, i.e. $Sp' \ll Ap'$ because of the hydrophobic nature of the unamended tailings sand and the very low amounts of organic matter, silt and clay (e.g. Table 3). Under these conditions, sorptivity (Sp') may be unimportant and infiltration controlled by $Ap' = K$ which is in fact very moisture dependent (Figure 33). The result is that, unlike agricultural soils, infiltration is facilitated by the soil being wet. Unless sorptivity is increased dramatically by soil amendments a dry soil will in fact be more erodable since $i/t \approx Ap \approx K$ of a dry sand may be much less than recorded storm intensities of 28 mm h^{-1}. The conclusion is that a moist sand may be necessary to prevent erosion.

Despite the apparent simplicity of the vascular flora at the Richardson site, the mycorrhizal associations are complex and varied. From fruiting body occurrence alone, more than 57 species of fungi were associated with Jack pine within a limited area. The large variety of symbionts was further substantiated by direct observation of mycorrhizae and cultural studies. These techniques failed to indicate that any one of several species of fungi dominated the below ground symbiotic system. The fungal partner of only a minority of the mycorrhizae observed in the field could be identified. The inability to match cultures from the dominant sporocarps to isolates from mycorrhizae appears to be the usual situation in some forest systems (Lamb and Richards 1970; Riffle 1973; Zak and Bryan (1963). However, Harvey et al. (1976) have reported that one morphological type of mycorrhizae dominated a mature douglas fir-larch forest in Montana.

The only previous report of pure culture syntheses with Jack pine were with *Thelephora terrestris* and *Psiolithus tinctorius* (Marx and Bryan 1970). Of the 14 species which formed mycorrhizae with pine in this study, only *Suillus tomentosus, Astraeus hygrometricus, Lactarius chelidonium, Tricholoma flavovirens, Cenococcum graniforme* and *Pisolithus tinctorius* produced structures distinctive enough to be recognized in the field. Synthesis tests with the unknown isolates showed that a variety of fungi produced the common non-descript type that dominated field samples. Therefore, direct observations of root systems may allow quantification of certain species but other techniques are necessary to identify and quantify species which produce mundane mycorrhizae. It should be noted that in culture several basidicarp isolates of *Suillus tomentosus* differed from the description given by Pantidou and Graves (1966). Clamps were very rare under all circumstances and occurred only on large diameter hyphae (5-6 μm).

It has been suggested that the hydnums were very likely mycorrhizal associates of conifers but confirmation has been lacking due to their stringent growth requirements. *Bankera fuligeneo-alba* in this study is the first confirmation of a hydraceous fungus as a mycorrhizal symbiont.

From the occurrence of fruit bodies, it would appear the hydnums become important only in mature forests and in localized areas. *Hydnellum peckii* frequently was observed forming fairy rings indicating a slow, progressive growth from an inoculum point. Hintikka and Naykki (1967) estimated that *Hydnellum ferrugineum* grew about 3 cm per year and was never found in disturbed areas or young stands, the same pattern that was observed at the Richardson site. Thus the hydnums occupy small islands of the forest root system in mature stands apparently limited to these sites by an extremely slow growth rate.

Mycorrhizal synthesis by *Coltrichia perennis* with Jack pine also represents the first confirmation of a mycorrhizal role of the terrestrial, stipitate polypores. In contrast to the hydnums, *Coltrichia* was typically found on bare disturbed soils. In that the mycorrhizae produced by *Coltrichia* are distinctive in appearance, they must be relatively rare or localized in occurrence as they were not observed on natural root systems.

It has been suggested that mycorrhizae may aid the host plant in water uptake thus helping it to avoid drought (Trappe 1977). Resistance to water movement is less in mycorrhizal oak seedlings than those not infected (Personal communication, Dixon, Garret and Cox 1980) resulting in higher leaf water potentials. Mycorrhizae could function to increase drought tolerance in ways other than simply increasing the range of water potentials in which water can be taken up by the plant. Mycorrhizae, particularly those with well developed rhizomorphs, may function as pipelines to increase the volume of soil being exploited and move water from a soil with high water potential to the roots where the water potential is low. Mycorrhizae are known to increase the logivity of feeder roots (Harley 1969), and they may also aid in survival during short periods of stress such as drought. Roots infected with the appropriate symbionts would then be able to respond to favourable moisture conditions once the droughty period had passed. These and other potential functions of the ectomycorrhizal remain to be evaluated.

In this study maximum linear growth occurred at the highest water potentials used with both NaCl and sucrose. In contrast Mexal and Reid (1973) found maximum growth of *Cenococcum* in liquid cultures to occur at 1.5 MPa. Uhlig (1972), who also used liquid cultures, found that five of the six mycorrhizal fungi he tested including *Tricholoma pessondatum*, grew best between -3.4 and -5.8 MPa. Working with the root pathogen *Phytophthora cinnamoni* Stern et al. (1976) found that the method of culture affected responses to osmotic potential. However, in their work *Phytophthora* was more tolerant to low water potentials on solid media than in liquid culture. Griffin (1972) concluded that linear extension was a satisfactory method to use in studies of water potential. Differences in the osmoticum used and cultural methods make comparisons between studies difficult. However, the data given here illustrate that some fungi, e.g. *Cenococcum*, are much more tolerant to low water potentials than other fungi such as *Laccaria*. Experiments on the water relations of the mycorrhizal fungi were of a preliminary nature only. Behaviour in culture where the transition from a high ψ to a low ψ is abrupt unlike the gradual transition in nature when the fungus is in a symbiotic situation may lead to erroneous conclusions. The question whether a good performer in pure culture behaves in a similar manner when mycorrhized remains to be tested.

The role of lichens, particularly *Cladina mitis*, may be quite important in the water balance of the Jack pine forest. Unlike vascular plants, lichens have no mechanism to control water uptake or loss; thus responding passively to the environment (Blum 1974). Previous workers (Jack 1935, Moul and Buell 1955, and Rouse and Kershaw 1971) have shown that lichens can act as an efficient barrier to water exchange between the atmosphere and the soil. The field studies showed that evaporation and the diurnal wet/dry cycle was the same as previously reported (e.g. Heatmole 1966) with maximum evaporation during the early afternoon and uptake at night. The results throughout the season agree with those of

Kershaw and Rouse (1971) in their study of *Cladina alpestris* (=*Cladina stellaris* in northern Ontario. The lichen carpet may be considered to be stratified with drying and wetting proceeding from the surface down. Gravimetric samples of the upper half of the carpet showed this to be the case. With drying, thallus water potentials decrease to very low values (Figure 16a). The wind tunnel experiments showed that at high water contents, resistance to water loss is low and evaporation is controlled by wind speed (Figure 16b). Control is transferred from the external wind to internal resistance with drying (Figure 16b). Larson and Kershaw (1976) calculated total resistance to water loss of 1.0×10^{-3} to 2.8×10^{-3} min cm^{-1} for *Cladina stellaris* at a windspeed of 1.6 m s^{-1}. These resistances are similar to those obtained for *Cladina mitis* at low water contents in the field and laboratory. The results agree with those of Kershaw and Rouse (1971) and Rouse and Kershaw (1971) in suggesting that the lichen layer is an effective barrier to water loss from the underlying soil an effect already mentioned as being important in water infiltration.

The effects of lichens on soil moisture due to interception are summarized in Tables 10a and 10b. The amount of precipitation retained may be as high as 1.844 mm h^{-1} depending upon the rainfall intensity. These figures (Table 10a) are lower than published figures, but cannot be directly compared since precipitation retention is at least a function of lichen layer thickness. Jack (1935) and Moul and Buell (1955) noted that many showers were not of sufficient duration or intensity to bring the lichen layer to field saturation, a condition necessary for penetration to the soil. At the Richardson site this was observed several times, i.e. the lichen layer prevented soil wetting (Table 16b). Thus the lichen layer prevents erosion by raindrop splash action, prevents some light showers from wetting the soil; yet tends to keep the soil moist by reducing evaporation.

Laboratory studies of Jack pine showed that while osmotic potential decreased with dehydration (Figure 18) there is no evidence of active osmotic adjustment. Further, the field measurements (Table 11) revealed a remarkably stable osmotic potential, but this is likely due to the fact that the trees were never stressed to any extent (Figure 23). The laboratory studies carried out on young trees suggest that net CO_2 assimilation is zero at ca. - 2.2 MPa ψ_{leaf} which is somewhat lower than the 1.5 MPa reported for lodgepole pine by Dykstra (1974), but not exceptionally low. Soybean NA is not zero until -2.4 MPa (Boyer 1970), nor is *Deschampsia*, an alpine grass, zero until -3.8 MPa (Johnson et al. 1974). Thus Jack pine is not exceptional in its ability to fix carbon at low water potentials a fact to be considered when selecting grasses as "nurse crops". Based upon the xylem tension measurements (Figure 23) NA would have never been less than 2 mg CO_2 $dm^{-2}h^{-1}$ (Figure 21) during the study. This is not to say that NA was not reduced by water relations since VPD induced stomatal closure obviously will reduce carbon fixation (Figure 26). Even if the photosynthetic capacity of pine is not particularly great, Jack pine is well adapted in that it avoids low ψ_{leaf} by VPD induced stomatal closure (Figure 26), can fix to fairly low ψ_{leaf} (Figure 21) and can recover from rather severe stress near -3.5 MPa (Figure 20). The mortality study (Figure 20) suggests the upper limit of xylem tension to be between 3.5 and 4.0 MPa depending upon duration. It was also noted that the younger stems and needles died first under stress, thus retaining the fully expanded more mature needles. This was observed on field trees as well. The strategy seems to be that photosynthetically mature tissue will be retained at the expense of the immature. It is felt that field trees would be at least as drought tolerant as the greenhouse trees (Figure 20).

The soil moisture tension, xylem tension, and needle water content data all show that in fact the trees studied at the Richardson site never suffered from moisture stress during the study (Figures 22 and 23). Jack pine is quite different in its year-round water relations compared with other species. The generally accepted paradigm holds that as a plant hardens in the fall, water content, water potential, and osmotic potential all decrease. According to Levitt (1972) "water content is frequently inversely related to hardiness." Water content usually decreases in the fall and may decrease more during the winter (e.g. McKenzie et al. 1974, Wilkinson 1977). Lowered osmotic potentials also associated with hardening. Wilkinson (1977) reports that *Ledum* $\psi_\pi + \psi_\tau$ lowers from -2.0 MPa in the summer to -6.5 MPa during the winter. Courtin and Mayo (1975) have summarized the reported ψ_π values for *Picea engellmanii, Picea pungens, Pinus cembra* and *Picea mariana*. The differences between summer and winter (winter always lower) are respectively 2.3, 1.3, 0.7 and 4.0 MPa. There is abundant evidence for fall and winter dehydration. Recently Cowling and Kedrowski (1980) have reported low needle xylem tensions in lodgepole pine in Alaska which agrees with our results for Jack pine (Figures 22, 23, Table 11). These show that Jack pine does not dehydrate with hardening and maintains high water content throughout the winter. Jack pine stomata reamin closed throughout the winter and only open as the soil warms in the spring (Figure 27). This agrees with the results of Cowling and Kedrowski (1980). Thus Jack pine is very resistant to winter dehydration and possibly more resistant to winter damage from pollutants such as SO_2 which gain entry via the stomates. This would be reduced during the winter because of dormancy induced stomatal closure.

VPD and xylem tension can both cause stomatal closure at PhAR values greater than 200 μEm^{-2} s^{-1} (Figures 24, 25, 26). Fetcher (1976) reports that lodgepole pine R_L is relatively insensitive to xylem tension between 0.9 and 1.7 MPa but is quite sensitive to VPD. Jack pine is relatively insensitive to xylem tension up to ca. 1.4 MPa. Exactly where xylem tension becomes important was not clearly determined since the trees were well watered. Pereira and Cozlowski (1977) report minimum leaf resistance for Jack pine of 5 s cm^{-1} which are similar to those at the Richardson site (Figures 24, 25, 26), though somewhat higher. They report 1.0 s cm^{-1} at 1.6 KPa VPD which agrees with the Richardson data. They do not report the sharp increase to ca. 35 s cm^{-1} shown as in Figure 26. Our results indicate that Jack pine stomata will close on hot dry days because of the VPD, thus tending to prevent high xylem tensions and to conserve soil moisture by reducing transpiration. This tendency plus the moisture conserving effect of the lichen layer tends to conserve soil moisture and help maintain it in a condition to conduct water.

The model of branch xylem tension (Figure 30) predicted values that were fairly close to measured values during the summer. Major differences occurred during June when night time recovery was in fact more rapid than predicted suggesting that resistances particularly in the tree root were less than expected. Otherwise agreement is quite good. Modelled max-min xylem tensions do not disagree greatly with the measured values (Figures 23, 31) and in terms of overall response, the model predicts tree behaviour quite well. It is unfortunate that the model was not validated under more stressful conditions nor was it used to develop responses of agronomic grasses on the dike. Never-the-less as developed it represents a very good start on the use of modelling in revegetation work. A start that should be pursued.

The Jack pine-lichen woodland is the dominant community in NE Alberta and NW Saskatchewan growing upon sand (Carroll and Bliss 1980). The "typical" successional of grasses → shrubs → trees does not take place on sands following disturbance (open dunes and burned forest). Grasses are very minor at all stages. This raises questions as to the advisability of revegetating mined sand with grasses. Stabilization is most frequently achieved by *Hudsonia tomentosa* a species under intense study at the University of Alberta. This plant appears to be the first pioneer on open sand followed by lichens and eventually pine.

7.0 CONCLUSIONS

The micrometeorological conditions within the Jack pine forest were monitored over two seasons. The years studied were fairly wet ones with frequent precipitation events (e.g. Figure 15). The site is somewhat warmer and drier than Fort McMurray (Figure 32, Table 12). The lack of intense storms probably accounts for the stability of such steep sand slopes. However, drier years do occur and storms of up to 28 mm h^{-1} have been recorded at Fort McMurray and at the Richardson site.

The persistence of steep sand slopes such as the Richardson site is primarily due to the very high hydraulic conductivity of the sand (Figures 7, 8, 33). Without such high porosity it is extremely doubtful if the sandhills would not be severely eroded. Water moves into the soil rapidly when wet, yet conductivity decreases rapidly with drying (Figures 8, 33). The combined lichen layer resistance to water loss plus the high R_L of Jack pine at high VPD (Figures 16b, 26, Table 10a) both conserve moisture tending to keep the sand wet, i.e. in a condition to rapidly conduct mositure, thus playing an important role in erosion prevention. The combination of high porosity plus lichen resistance to evaporation and Jack pine high R_L seems to be quite important.

The mycorrhizal flora of the Richardson site is much more varied than the higher plant flora (Table 6). There appear to be differences associated with succession from a burned area to a more stable community (Table 7). The great diversity suggests more of a role in the community than is presently understood and offers opportunity for further work. The mycorrhizal fungi associated with a particular species may be highly important in its success upon a stressful site.

Cladina mitis was the major lichen at the Richardson site. The lichen community was described and its very important role in moisture conservation discussed above. The lichens also are important in absorbing raindrop impact thus helping to control erosion.

Jack pine is well adapted to the sandy, nutrient poor sites on which it grows because: 1) it avoids winter and spring drought by maintaining high leaf resistances during the periods when frozen soils might limit water uptake (Figures 23, 27); 2) it does not cavitate under freeze thaw conditions (Wilkinson 1977), thus maintaining intact xylary water columns; 3) its stomata are sensitive to atmospheric VPD (Figure 26), thus closing prior to xylem tension or ψ_{leaf} induced closure. This is important in conserving soil moisture by maintaining high R_L values on hot-dry days; 4) it exhibits at least passive osmotic adjustment to dehydration thus tending to absorb more water from drier soils (Figure 18); 5) it does not dehydrate upon hardening for winter, thus carrying more tissue water into and through the winter (Figures 22, 23), winter and spring drought were not a problem; 6) Carbon fixation is positive to -2.2 MPa ψ_{leaf} thus allowing fixation under moderate drought stress and photosynthetic capacity is restored upon relief (Figure 21); 7) in the event of extreme drought, the more mature photosynthetically active tissue is retained at the expense of the younger (non-self-sufficient) tissue, and death does not occur until 3.5 to 4.0 MPa xylem tension (Figure 20); 8) while nutrients were not studied, Jack pine has low amounts of N, P, K, Ca and Mg compared with aspen, red pine and white spruce on similar soils (Alban, Perala, and Schlaegel 1978), and according to Morrison (1973) is less N, P, K, Ca and Mg demanding than white pine, red pine or white spruce. Morrison (1973) states: "Presumably then, it is this low nutrient requirement which enables Jack pine to maintain acceptable growth rates on sites of low fertility." The modelling effort while truncated was successful. A working radiation model was developed (Figures 28, 29) and the water balance model does predict diurnal and seasonal trends in water relationships (Figures 30, 31). The modelling was successful enough thaturther work, validating under higher stress conditions and adaptions to the dike-agronomic grasses are entirely warranted.

8.0 RECOMMENDATIONS

While recognizing that the results of the study of the Jack pine-lichen woodland at the Richardson firetower are not absolutely definitive concerning rehabilitation of mined sands, the following facts are considered to be important: 1) the sandy soil-lichen layer-Jack pine forest functions as a unit such that water is conserved at the same time that high soil water conductivity is maintained thus preventing erosion; 2) because of the combined characteristic behaviour of the system, treatments resulting in the change in the properties of one of these three characteristics may change the others resulting in instability. These points should be kept in mind when considering the following:

1. The maintenance of high soil infiltration capacity is absolutely essential if dike erosion is to be prevented. Peat amended tailings sand may have a higher saturated conductivity than the unamended sand, however if grasses are used and grass roots are confined to the amended layer (Rowell 1977) the peat amended layer will be quite dry much of the time because of the high transpiration rate. This may in fact reduce infiltration capacity (Figure 33) resulting in overland flow and erosion (Rowell 1977, p. 28, Rowell 1977, p. 50).
2. The lichen-layer-Jack pine vegetation tend to conserve water and keep the soil moist for the reasons mentioned in the discussion and conclusions. This tends to maintain a high infiltration capacity. If the lichen layer is destroyed or not present and pine replaced with other species and the tailings sand amended (i.e. the dike situation), the sorptivity of the soil must be increased considerably so that infiltration is high enough to prevent overland flow. In the infiltration equation (Taylor and Ashcroft 1972)

   $$i = Sp't^{\frac{1}{2}} + Ap't$$

   where i = infiltration
   Sp' = sorptivity
   Ap' = approximately saturated conductivity
   t = time,

   the pine-lichen situation is $Ap' \gg Sp'$, by amending the soil Sp' becomes more important, however if as stated under #1 above, the grasses dry the amended layer conductivity can be decreased. Thus Sp' must be increased much more, i.e. not just a little (i.e. $Sp' \gg Ap'$).

3. The role of mycorrhizae is not well understood yet the diversity of the mycorrhizal flora at the firetower site suggests that which fungal symbiont is associated with the revegetation species can be highly important. Work on this problem should (and I understand is) continue.

4. The role of lichens in the overall water budget of the Richardson site is considered to be very important in reducing raindrop impact and as an effective mulch greatly reducing evaporation of soil water. The use of mulches that approximate the lichen layer may be useful. The effects of pollutants upon the lichen layer of the Jack pine woodlands is and should be monitored closely in view of its role in erosion control and moisture conservation.

5. The ecophysiologic characteristics of Jack pine illustrating its adaptation to xeric, nutrient poor sites should be borne in mind when selecting potential revegetation species. It provides a standard of comparison. The following are important:

   a) its low nutrient requirements (already discussed under conclusion) means that it is well adapted to the mined sands and unless fertilization is carried out indefinitely and/or cation exchange capacity is improved dramatically, species with low nutrient requirements are essential. It is known that Jack pine will respond to fertilizer and can benefit from sewage effluent (Tolsted 1976). It is also sensitive to fertilizer and too much will reduce growth (McClain and Annson 1975). Thus fertilizer sufficient for growth of agronomic grasses (e.g. George et al. 1973) may reduce growth of Jack pine, black and white spruce. These grasses may not be good nurse crops for trees.

   b) Jack pine resists winter and spring moisture stress by entering winter fully hydrated with closed stomata (Figures 23, 27), the stomata remain tightly closed until well after melt out. Other species avoid winter and spring stress by shedding their leaves but at the apparent expense of higher nutrient requirements.

c) Jack pine tends to avoid summer moisture stress (Figure 26) by closing its stomata on hot-dry (high VPD) days. As mentioned above this trait works with the lichen layer to conserve moisture and maintain high soil water conductivity (Figures 26, 34, Table 10).

d) Jack pine can fix carbon to -2.2 MPa ψ_{leaf} (Figure 21). This is considerably lower than many tress, e.g. *Pinus contorta* NA = 0 at -1.5 MPa (Dykstra 1974) even though not particularly low. Revegetation species should be at least this good.

e) Jack pine can survive extended drought during which time ψ_{leaf} goes to -3.5 or 4.0 MPa. This is considerably lower than stresses tolerated by many agronomic species. An important consideration is that if drought hardy grasses are used as a nurse crop they may dry the soil more than pine can tolerate and thus prevent reforestation without providing enough soil protection (see 1 and 2 above).

6. It should be borne in mind that grasses do not make up an important component of the vegetation found on sands in the Fort McMurray region (Carroll and Bliss 1980).
7. Modelling while curtailed due to the project termination does offer an efficient means of testing revegetation schemes. If the models developed were validated under more stressful conditions and adapted (along with appropriate physiological experiments) to the dike-agronomic grass situation, they would provide an effective guide to rehabilitation work.

9.0 REFERENCES CITED

Bannan, M.W. 1940. The root systems of Northern Ontario conifers growing in sand. Am. J. Bot. 27: 108-114.

Baumgartner, A. 1965. The heat, water and carbon dioxide budget of plant cover: methods and measurements. Methodology of plant ecophysiology. Proceedings of the Montpellier Symposium, p 495-512. Paris, Unesco (Arid Zone Research, XXV).

Bennett, K.J., and D.A. Rook. 1978. Stomatal and mesophyll resistances in two clones of *Pinus radiata* D. Don known to differ in transpiration and survival rate. Aust. J. Plant Physiol. 5: 231-238.

Bergen, J.D. 1969. Cold air drainage on a forested mountain slope. J. Appl. Meteorol. 8: 884-895.

Bergen, J.D. 1971. Topographic effects apparent in nocturnal temperature profiles in a conifer canopy. Agric. Meteorol. 9: 39-50.

Bliss, L.C. (ed.) 1977. Long term prediction of vegetation performance on mined sands. AOSERP Interim Report. 272 pp.

Bliss, L.C. (ed.) 1979. Performance of vegetation on mined sands. AOSERP Report. 251 pp.

Blum, O. 1974. Water relations. p. 381-400 in M.E. Hale and V. Ahmadjian eds. The Lichens. Academic Press, N.Y.

Boyer, J.S. 1970. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. Plant Physiol. 86: 236-239.

Brace, J.P. 1959. Rainfall intensity - duration - frequency maps for Canada. Meteorological Branch, Dept. of Transport Technical Circular 308. 9 pp.

Bremner, J.M. 1965. Total nitrogen. p. 1149-1178 in C.A. Black, ed. Methods of Soil Analysis. Agron. No. 9, Amer. Soc. Agron. Madison, Wisc.

Brown, P.S., and J.P. Pandalfo. 1969. An equivalent-obstacle model for the computation of radiative flux in obstructed layers. Agr. Meteorol. 6: 407-421.

Bundy, L.G., and J.M. Bremner. 1972. A simple titrimetric method for determination of inorganic carbon in soils. Soil Sci. Soc. Amer. Proc. 36: 273-275.

Calder, I.R. 1977. A model of transpiration and interception loss from a spruce forest in Plynlimos, Central Wales. J. of Hydrology 38: 33-47.

Calvert, R.F., and K.A. Armson. 1975. The growth response of young Jack pine to nitrogen and phosphorus. Can. J. For. Res. 5: 529-538.

Canadian Society of Soil Science. 1975. Manual on soil sampling and Methods of Analysis. Prep. by Subcommittee of Canada Soil Survey Committee on Methods of Analysis.

Carbon, B.A. 1975. Redistribution of water following precipitation on previously dry sandy soils. Aust. J. Soil Res. 13: 13-19.

Carroll, Steve and L.C. Bliss. 1980.

Cheyney, E.G. 1932. The roots of a Jack pine tree. Journ. Forest. 30: 939-932.

Cochran, P.H. 1972. Temperature and soil fertility effect lodgepole and Ponderosa pine seedling growth. Forest Sci. 18: 132-134.

Cook, F.D., ed. 19 . Soil Research Related to Vegetation of the Oil Sands Area. AOSERP Subproject. VE4. pp. 10-14.

Courtin, G.M., and J.M. Mayo. 1975. Arctic and alpine plant water relations. Pages 201-221 in F. John Vernberg, ed. Physiological Adaptation to the Environment. Intext Educational Publishers N.Y.

Cowling, J.E., and R.A. Kedrowski. 1980. Winter water relations of native and introduced evergreens in interior Alaska. Can. J. Bot. 58: 94-99.

Dykstra, G.F. 1974. Photosynthesis and carbon dioxide transfer resistance of lodgepole pine seedlings in relation to irradiance, temperature, and water potential. Can. J. For. Res. 4: 201-206.

Edean, F., and L.W. Carlson. 1975. The effect of rooting volume on the early growth of lodgepole pine seedlings. Can. J. For. Res. 5: 55-60.

Edgington, L.V., K.L. Khew, and G.L. Barron. 1971. Fungi-toxic spectrum of benzimidazole compounds. Phytopathology 61: 42-44.

Elrick, D.E. 1963. Unsaturated flow properties of soils. Aust. J. Soil Res. 1: 1-8.

Elrick, D.E., and D.H. Bowman. 1964. Note on an improved apparatus for soil moisture flow measurements. Soil Sci. Soc. Amer. Proc. 28: 450-452.

Farquhar, G.D. 1978. Feedforward responses of stomata to humidity. Aust. J. Plant Physiol. 5: 787-800.

Fetcher, N. 1976. Patterns of leaf resistance to lodgepole pine transpiration in Wyoming. Ecology 57(2): 339-345.

Foster, N.W. 1974. Annual macroelement transfer from *Pinus banksiana* Lamb. forest to soil. Can. J. For. Res. 4: 470-476.

Foster, N.W., and S.P. Gessel. 1972. The natural addition of nitrogen, potassium and calcium toto a *Pinus banksiana* Lamb. forest floor. Can. J. For. Res. 2: 448-455.

Galoux, A. 1971. Flux et transferts d'énergie au niveau des écosystèmes forestiers. In Productivité des écosystèmes forestiers, Actes Coll. Bruxelles 1969. (UNESCO (Ecologie et conservation, 4).

Gardner, W.R., W.A. Jury, and J. Knight. 1975. Water uptake by vegetation. Ch. 30. in D.A. deVries and N.H. Afgan, eds. Heat and Mass Transfer in the Biosphere. Scripta Book Co., Washington.

Gates, D.M., E.C. Tibbals, and F. Kreith. 1965. Radiation and convection for ponderosa pine. Amer. J. Bot. 52: 66-71.

Gay, L.W. 1972. Energy flux studies in a coniferous forest ecosystem. Pages 243-253 in J.F. Franklin, L.J. Dempster and R.H. Waring, eds. Proceedings - Research on Coniferous Forest Ecosystems. A Symposium. Portland, Oregon.

Geiger, R. 1965. The Climate Near the Ground. Howard Univer. Press, Cambridge, Mass. 611 pp.

George, J.D., C.L. Rhykerd, C.H. Noller, J.E. Dillon, and J.C. Furus. 1973. Effect of N fertilization on dry matter yield, total N, N recovery and nitrate-N concentration of three cool-season forage grass species.

Glerum, C. 1973. Annual trends in frost hardiness and electrical impedance for seven coniferous species. Can. J. Plant Sci. 53: 881-889.

Gloyne, R.W. 1965. A method for calculating the angle of incidence of direct beams of the sun on a plane surface of any slope and aspect. Agr. Meteorol. 2: 401-410.

Goudriian, J., and P.E. Waggoner. 1972. Simulating both aerial microclimate and soil temperature from observations above the foliar canopy. Neth. J. Agric. Sci. 20: 104-124.

Green, R.E., and . Corey. 1971. Calculation of hydraulic conductivity: a further evaluation of some predictive models. Soil Sci. Soc. Amer. Proc. 35: 3-8.

Gresham, C.A., T.R. Sinclair, and J.E. Wuenscher. 1975. A ventilated diffusion porometer for measurement of the stomatal resistance of pine fascicles. Photosynthetica 9: 72-77.

Griffin, D.M. 1972. Ecology of soil fungi. Syracuse University Press.

Hacskaylo, E. 1965. *Thelephora terrestris* and mycorrhizae of Virginia pine. For. Sci. 11: 401-404.

Hage, K., C. Labine, and G. Reynolds. 1977. Micrometeorology. Pages 12-38 in L.C. Bliss, ed. Long term prediction of vegetation performance on mined sands. Report to Alberta Oil SAnds Environmental Research Programme. Project VE6.1.

Hall, A.E., E.-D. Schulze, and O.L. Lange. 1976. Current perspectives of steady-state stomatal responses to environment. Pages 170-188 in O. Lange, ed. Ecological Studies Analysis and Synthesis. Vol. 19.

Harley, J.L. 1969. The Biology of Mycorrhizae. Leonard Hill, London.

Harrison, K.A. 1971. The evolutionary lines in the fungi with spines supporting the hymenium. Pages 375-388 in R.H. Petersen, ed. Evolution in the Higher Basidiomycetes. Univ. Tenn. Press, Knoxville.

Harvey, A.E., M.J. Larsen, and M.F. Jurgasen. 1976. Distribution of ectomycorrhizae in a mature Douglas fir/larch forest soil in Western Montana. For. Sci. 22: 393-398.

Heatmole, H. 1966. Moisture exchange between the atmosphere and some lichens of the genus *Cladonia*. Mycologia 58: 148-156.

Hintikka, V., and O. Naykki. 1967. Notes on the effects of the fungus *Hydnellium ferrigeneum* (Fr.) Korst. on forest soil and vegetation. Comm. Inst. For. Fen. 62(2): 1-22.

Hocking, D., and D.L. Mitchell. 1975. The influence of rooting volume-seedling espacement and substratum density on greenhouse growth of lodgepole pine, white spruce, and Douglas fir grown in extruded peat cylinders. Can. J. For. Res. 5: 440-451.

Höfler, K. 1920. Ein schema fur die osmótische Leistung der Pflanzenzelle. Ber. Deutsch. Bot. Ges. 38: 288-298.

Hutchison, B.A. 1979. Forest Meteorology - research needs for an energy and resource limited future. Proceedings of a workshop. Ottawa, 1978.

Jack, H.A. 1935. Precipitation retention by *Cladonia* mats. Ecology 16: 120-121.

Jarvis, P.G. 1975. Water transfer in plants. Ch. 25 in D.A. deVries and N.H. Afgan, eds. Heat and Mass Transfer in the Biosphore. Scripta Book Co., Washington, D.C.

Jarvis, P.G. 1976. The interpretations of the variations in leaf water potential and stomatal conductance found in canopies in the field. Phil. Trans. R. Soc. Lond. B. 273: 593-610.

Jarvis, P.G., G.B. James, and J.J. Landsberg. 1976. Coniferous Forest. Vol. 2 in J.L. Monteith, ed. Vegetation and the Atmosphere. Academic Press, New York.

Johnson, D.A., M.M. Caldwell, and L.L. Tieszen. 1974. Photosynthesis in relation to leaf ψ in 3 alpine species. In F.E. Wielgolaski and L.C. Bliss, eds. Proc. I.B.P. Tundra Biome Primary Production Meeting, 1973. Dublin, Ireland.

Kershaw, K.A., and W.R. Rouse. 1971. Studies on lichen dominated systems. I. The water relations of *Cladonia alpestris* in spruce-lichen woodland in northern Ontario. Can. J. Bot. 49: 1389-1399.

Kilmer, V.J., and L.T. Alexander. 1949. Methods of making mechanical analyses of soils. Soil Sci. 68: 15-24.

Kittredge, J. 1948. Forest Influences. Dover Publications, New York. 394 pp.

Klute, A. 1965. Laboratory measurement of hydraulic conductivity of saturated soil. Pages 210-221 in C.A. Black, ed. Methods of Soil Analysis, part 1. Agron No. 9, Amer. Soc. Agron. Madison, Wisc.

Korven, ., and . Taylor. 1959. Determining activity of soil water. Can. J. Soil Sci. 39: 76-85.

Kozlowski, T.T. 1968. Water Deficits and Plant Growth. Academic Press.

Laiho, P. 1970. *Paxillus involutus* as a mycorrhizal symbiont of forest trees. Acta Forest. Fenn. 106: 1-72.

Lamb, R.J., and B.N. Richards. 1970. Some mycorrhizal fungi of *Pinus radiata* and *P. elliottii* var. *elliottii* in Australia. Trans. Brit. Mycol. Soc. 50: 371-378.

Landsberg, J.J., and A.S. Thom. 1971. Aerodynamic properties of a plant of complex structure. Quart. J. Roy. Met. Soc. 97(414): 565-570.

Landsberg, J.J., and P.G. Jarvis. 1973. A numerical investigation of the momentum balance of a spruce forest. J. Appl. Ecol. 10: 645-655.

Larson, D.W., and K.A. Kershaw. 1976. Studies on lichen dominated systems. XVIII. Morphological control of evaporation in lichens. Can. J. Bot. 54: 2061-2073.

Legge, A.H., G.W. Harvey, P.F. Lester, D.R. Jaques, H.R. Krouse, J. Mayo, A.P. Hartgerink, R.G. Amundson, and R.B. Walker. 1976. Quantitative assessment of the impact of sulfur gas emission on a forest ecosystem. A final report submitted to the Whitecourt Environmental Study Group, Environmental Science Centre (Kananaskis).

Levitt, J. 1972. Response of Plants to Environmental Stresses. Academic Press, N.Y.

List, R.J. 1966. Smithsonian Meteorological Tables. Smithsonian Institute, Washington, D.C.

Logan, K.T. 1971. Monthly variations in photosynthetic rate of Jack pine provenances in relation to their height. Can. J. For. Res. 1: 256-261.

Lopushinsky, W., and G.O. Klock. 1974. Transpiration of conifer seedlings in relation to soil water potential. Forest Sci. 20: 181-186.

Marx, D.H. 1969. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. Phytopathology 59: 153-163.

Marx, D.H. 1976. Synthesis of ectomycorrhizae on loblolly pine seedlings with basidiospores of *Pisolithus tinctorius*. For. Sci. 22: 13-20.

Marx, D.H., and W.C. Bryan. 1970. Pure culture synthesis of ectomycorrhizae by *Thelephora terrestris* and *Pisolithus tinctorius* on different conifer hosts. Can. J. Bot. 48: 639-643.

Mayo, J.M. 1974. A thermocouple psychrometer chamber for field and laboratory use. Can. J. Plant Sci. 54: 597-598.

McKenzie, J.S., D.J. Weiser, and P.H. Li. 1974. Changes in water relations of *Cornus stolonifera* Mich. Plant Physiol. 53: 783-789.

Mclain, K.M., and K.A. Armson. 1975. Growth responses of pine and spruce seedlings to regimes of soil moisture and fertility. Soil Sci. Soc. Amer. Proc. 39: 140-144.

Mexal, J., and C.P.P. Reid. 1973. The growth of selected mycorrhizal fungi in response to induced water stress. Can. J. Bot. 51: 1579-1588.

Mehlenbacher, L.A., and D.W.A. Whitfield. 1977. Modelling thermal eddy diffusivity at canopy height. Boundary-Layer Meteorol. In Press.

Mikalo, P. 1973. Application of mycorrhizal symbiosis in forestry practice. Pages 383-411 in G.C. Marks and T.T. Kozlowski, eds. Ectomycorrhizae - Their Ecology and Physiology. Academic Press, N.Y.

Mikalo, P. 1970. Mycorrhizal inoculation in afforestation. Int. Rev. For. Res. 3: 123-196.

Miller, O.K. 1962. Mushrooms of North America. Dutton, N.Y.

Millington, R.J., and J.P. Quirk. 1961. Permeability of porous solids. Trans. Faraday Soc. 57: 1200-1207.

Mitchell, J.A. 1930. Interception of rainfall by the forest. J. For. 37: 101-102.

Monsi, M., Z. Uchijima, and T. Oikawa. 1973. Structure of foliage canopies and photosynthesis. Pages 424 in B.F. Johnston, ed. Annual Revue of Ecology and Systematics. Ann. Rev. Inc.

Morrison, I.K. 1972. Variation with crown positions and leaf age in content of seven elements in leaves of *Pinus banksiana* Lamb. Can. J. For. Res. 2: 89-94.

Morrison, I.K. 1973. Distribution of elements in aerial components of several natural Jack pine stands in Northern Ontario. Can. J. For. Res. 3: 170-179.

Morrison, I.K. 1974. Dry-matter and element content of roots of several natural stands of *Pinus banksiana* Lamb. in Northern Ontario. Can. J. For. Res. 4: 61-64.

Moul, E.T., and M.F. Buell. 1955. Moss cover and rainfall interception in frequently burned sites in the New Jersey pine barrens. Bull. Torrey Bot. Club 82: 155-162.

Mukammal, E.J. 1971. Some aspects of radiant energy in a pine forest. Archiv. Met. Geophysk. Bioklimt. B, 19: 29-52.

Murphy, C.E., and K.R. Knoerr. 1975. The evaporation of intercepted rainfall from a forest stand: an analysis by simulation. Water Resour. Res. 11: 273-280.

Murray, F.W. 1967. On computation of saturation vapor pressure. J. Appl. Meteorol. 6: 203-204.

Nilson, T. 1971. A theoretical analysis of the frequency of gaps in plant stands. Agr. Meteorol. 8: 25-38.

Nobel, P.S. 1974. Introduction to biophysical plant physiology. W.H. Freeman and Co., San Francisco. pp. 304-305.

Norman, J.M., and P.G. Jarvis. 1974. Photosynthesis in Sitka spruce. III. Measurements of canopy structure and interception of radiation. J. Appl. Ecol. 11: 375-398.

Norman, J.M., and P.G. Jarvis. 1975. Photosynthesis in Sitka spruce. V. Radiation penetration theory and a test case. J. Appl. Ecol. 12: 839-878.

Oikawa, T., and T. Saeki. 1972. Light regime in relation to population structure - an experimental approach based on the Monte Carlo simulation model. Rep. 1971 IBP/PP Photosynthesis Level III Group. Tokyo. p 107-116.

Pantidou, M.E., and J.W. Groves. 1966. Cultural studies of boletaceae. Some species of *Suillus* and *Fuscoboletinus*. Can. J. Bot. 44: 1371-1392.

Pereira, J.S., and T.T. Kozlowski. 1977. Water relations and drought resistance of young *Pinus banksiana* and *P. resinosa* plantation trees. Can. J. For. Res. 7(1): 132-137.

Philip, J.R. 1957. The theory of infiltration: the sorptivity and algebraic infiltration equations. Soil Sci. 84: 257-264.

Raup, H.M. 1935. Botanical Investigations in Wood Buffalo Park. Can. Dept. Mines, Nat. Mus. Canada. Bull. 74. Ottawa. 174 pp.

Richards, L.A. 1949. Methods of measuring soil moisture tension. Soil Sci. 68: 95-112.

Riffle, J.W. 1973. Pure culture synthesis of ectomycorrhizae on *Pinus ponderosa* with species of *Amanila, Suillus*, and *Lactarius*. For. Sci. 19: 242-250.

Ritchie, G.A., and T. Hinckley. 1975. The pressure chamber as an instrument for ecological research. Adv. Ecol. Res. 9: 166-255.

Roberts, F.J. 1966. The effects of sand type and fine particle amendments on the emergence and growth of subterranean clover with particular reference to water relations. Aust. J. Agric. Res. 17: 657-672.

Robinson, R.A., and R.H. Stokes. 1955. Electrolyte solutions. Academic Press, N.Y.

Rose, C.W., W.R. Stern, and J.E. Drummond. 1965. Determination of hydraulic conductivity as a function of depth and water content for soil in situ. Aust. J. Soil Res. 3: 1.

Ross, J. 1975. Radiative transfer in plant communities. Page 278 in J.L. Monteith, ed. Vegetation and the Atmosphere, Vol. 1. Principles. Academic Press, N.Y.

Rouse, W.R., and K.A. Kershaw. 1971. The effects of burning on the heat and water regimes of lichen-dominated subarctic surfaces. Arct. Alp. Res. 3: 291-304.

Rowe, J.S. 1959. Forest Regions of Canada. Dept. Nor. Affairs and Nat. Resources. Forestry Branch. Bull. 123. Ottawa. 71 pp.

Rowe, J.S., and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Res. 3: 444-464.

Rowell, M.J. 1977. Continued studies of soil improvement and revegetation of tailings sand slopes. Environmental Research Monograph 1977-4. Syncrude Canada Ltd. 156 pp.

Rowell, M.J. 1978. Revegetation and management of tailings sand slopes: 1977 results. Environmental Research Monograph 1978-5. Syncrude Canada Ltd. 125 pp.

Rowell, M.J. 1979. Revegetation and management of tailings sand slopes from tar sand extraction: 1978 results. Environmental Research Monograph 1979-5. Syncrude Canada Ltd. 150 pp.

Russell, F.W. 1961. Soil conditions and plant growth. Longmans, London.

Salter, P.J., G. Berry, and J.B. Williams. 1967. The effects of farmyard manure on matric suctions prevailing in sandy loam soil. J. Soil Sci. 18: 318-328.

Sceicz, G. 1974. Solar radiation for plant growth. J. Appl. Ecol. 11: 617-636.

Schramm, J.E. 1966. Plant colonization studies on black wastes from anthracite mining in Pennsylvania. Amer. Philso. Soc. 56: 1-194.

Selner, J., and R. Thompson. 1977. Reclamation for afforestation by suitable native and introduced tree and shrub species. AOSERP Report VE. 7.1. 93 pp.

Sheriff, D.W. 1977. The effect of humidity on water uptake by and viscous flow resistance of excised leaves of a number of species: Physiological and Anatomical observations. J. Expt. Bot. 28(107): 1399-1407.

Singer, R. 1975. The Agaricales in Modern Taxonomy. J. Cramer, Vaduz, Germany.

S

Slavik, B. (ed.) 1974. Methods of Studying Pl ant Water Relations. Academic Pub. House, Prague. 449 p.

Smith, H.V., and A.H. Smith. 1973. How to Know the Non-gilled Fleshy Fungi. Wm. C.Brown, Dubuque.

Stack, R.W., W.A. Sinclair, and A.O. Larsen. 1975. Preservation of basidiospores of *Laccaria laccata* for use as mycorrhizal inoculum. Mycologia 67: 167-170.

Sterne, R.E., G.A. Zentmyer, and F.T. Bingham. 1976. The effect of osmotic potential and specific ions on growth of *Phytophthora cinnamoni*. Phytopathology 66: 1398-1402.

Stewart, J.B., and A.S. Thom. 1973. Energy budgets in pine forest. Quart. J. Roy. Met. Soc. 99(419): 154-170.

Stringer, P.W. 1976. A preliminary vegetation survey of the Alberta Oil Sands area. AOSERP Report.

Takyi, S.K., M.H. Rowell, W.B. McGill, and M. Nyborg. 1977. Reclamation and vegetation of surface mined areas in the Athabasca tar sands. Environmental Research Monograph 1977-1. Syncrude Canada Ltd. 170 pp.

Tanaka, S. 1968. Estimation of sunlit leaf area in a tobacco community by Monte Carlo method (1) Estimation of direct sunlight of a plant. Environ. Control Biol. 7: 12-16. (In Japanese)

Taylor, J.B. 1971. A selective medium for the isolation of basidiomycetes from diseased roots, mycorrhizae and soil. Bot. Rev. 28: 538-606.

Taylor, S.A., and G.L. Ashcroft. 1972. Physical Edaphology. W.H. Freeman and Co., San Francisco. p 209, p 211-218.

Thom, A.S., J.B. Stewart, H.R. Oliver, and J.H.C. Gash. 1975. Comparison of aerodynamic and energy budget estimates of fluxes over a pine forest. Quart. J. Roy. Met. Soc. 101(427): 93:105.

Thompson, F.B., and L. Layton. 1971. Method for measuring the leaf surface area of complex shoots. Nature 229: 572.

Tolsted, D.N. 1976. Sewage effluent spray increases diameter growth of Jack pine. U.S.D.A. Forest Service Res. Note, No. NC-207, North Central Forest Expt. Station.

Toogood, J.A., and T.W. Peters. 1953. Comparison of methods of mechanical analysis of soils. Can. J. Agr. Sci. 33: 159-171.

Trappe, J.M. 1962. Fungus associates of ectotrophic mycorrhizae. Bot. Rev. 28: 538-606.

Trappe, J.M. 1967. Pure culture synthesis of Douglas-fir mycorrhizae with species of *Hebeluna, Suillus, Rhizopogon,* and *Astraeus*. For. Sci. 13: 121-130.

Trappe, J.M. 1971. Mycorrhizae-forming ascomycetes. Pages 19-37 in E. Hacskaylo, ed. Mycorrhizae. U.S.O.R. Misc. Publ. 1189.

Trappe, J.M. 1977. Selection of fungi for ectomycorrhizal inoculation in nurseries. Ann. Rev. Phytopathol. 15: 203-222.

Ulig, S.K. 1972. Investigations on drought resistance of mycorrhizae forming fungi. Zentrdbl. Bakt. Parwitenk. Inekt. Hyg. Abt. 2, 127: 124-132.

Vaartnou, H. 1976. Revegetation research. AOSERP Report VE.7.2-7.4. 350 pp.

Webb, R.A. 1972. Use of the boundary line in the analysis of biological data. J. Hort. Sci. 47: 309-319.

Webster, R. 1966. The measurement of soil water tension in the field. New Phytol. 65: 249-258.

Webster, R., and P.H.T. Bakett. 1971. Matric suctions to which soils in south central England drain. J. Agr. Sci. 78: 379-387.

Whistance-Smith, R. 1973. Rainfall measurement of Edmonton, Alberta. A comparison of two network density scales. M.Sc. Thesis, University of Alberta, Edmonton.

Wilkinson, A.J. 1977. Physiological aspects of cold hardiness of *Ledum groenlandicum*. M.Sc. Thesis, U niversity of Alberta, Edmonton, Alberta. 150 pp.

Winston, P.W., and D.H. Bates. 1960. Saturated solutions for the control of humidity in biological research. Ecology 41: 232-237.

Yeatman, C.W., and M.J. Holst. 1972. Hardiness of Jack pine hybrids and provenances in the boreal forest. Forest Chron. 4: 30-31.

Zak, B. 1973. Classification of ectomycorrhizae. Pages 43-78 in G.C. Marks and T.T. Kozlowski, eds. Ectomycorrhizae - their Ecology and Physiology. Academic Press, N.Y.

Zak, B. 1976. Pure culture synthesis of bearberry mycorrhizae. Can. J. Bot. 54: 1297-1305.

Zak, B., and W.C. Bryan. 1963. Isolation of fungal symbionts from pine mycorrhizae. For. Sci. 9: 270-278.

Zak, B., and D.H. Marx. 1964. Isolation of mycorrhizal fungi from roots of individual slash pines. For. Sci. 10: 214-222.

10.0 APPENDICES

Table 13. A list of vascular plant species collected within the study plots at the Richardson Firetower.

Trees

Betula papyrifera Marsh.
Pinus banksiana Lamb.
Populus tremuloides Michx.

Shrubs

Alnus crispa (Ait.) Prush
Amelanchier alnifolia (Nutt.) Nutt.
Arctostaphylos uva-ursi (L.) Spreng.
Hudsonia tomentosa Nutt.
Lonicera involucrata (Richards.) Banks
Prunus virginiana Nutt.
Rosa acicularis Londl.
Symphoricarpos albus (L.) Blake
Vaccinium myrtillus L.
Vaccinium vitis-idaea L.

Herbs

Anemone canadensis L.
Arceuthobium americanum Nutt.
Artemisia campestris L.
Aster ciliatus (Ledeb.) Fedtsch.
Calamagrostis rubescens Buckl.
Campanula rotundifolia L.
Carex sp.
Galium boreale L.
Hieracium umbellatum L.
Maianthemum canadense L.
Muhlenbergia cuspidata Lindl.
Saxifraga tricuspidata Rottb.
Solidago gigantea Ait.